THE GENUS *THEOPE* AND RELATIVES: THEIR SYSTEMATICS AND BIOLOGY (LEPIDOPTERA: RIODINIDAE: NYMPHIDIINI)

By

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In loving memory of my father
John Wilton Hall,
who nurtured my passion for
natural history

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Abstract of Dissertation Presented to the Graduate School
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THE GENUS *THEOPE* AND RELATIVES: THEIR SYSTEMATICS AND BIOLOGY (LEPIDOPTERA: RIODINIDAE: NYMPHIDIINI)

By

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A revision of the Neotropical nymphidiine riodinid genus *Theope* Doubleday, 1847, is presented which includes detailed taxonomic and ecological notes, distributional data for all taxa, a key to all species, and illustrations of adults and the abdominal, and male and female genitalic morphology for all species. The early stage biology, adult ecology, particularly male perching behavior, biogeography, and taxonomic history of the genus are discussed. The genera *Parnes* Westwood, 1851, and *Dinoplotis* Stichel, 1911, are synonymised with *Theope*, and two new species and two new subspecies are described: *Theope nodosus* n. sp., *Theope pseudopedias* n. sp., *Theope matuta heureka* n. ssp., and *Theope publius incompositus* n. ssp.. The following species are newly brought into combination with *Theope*: *nycteis* Westwood, 1851, *brevignoni* Gallard, 1996, *philotes* Westwood, 1851, *orphana* Stichel, 1911, and *antanitis* Hewitson, 1874. A number of taxonomic changes are made at the species level and below, and 68 species are recognised in the genus; 15 lectotypes are designated. Two species, *drepana* Bates, 1868, and *urichi* Vane-Wright, 1994, are transferred from *Theope* to the new genus *Archaeonympha* Hall, 1998. This genus is reviewed and its systematic position discussed.

Based on preliminary cladistic analyses, I propose merging the riodinid tribes Nymphidiini Bates, 1859, and Lemoniadini Kirby, 1871 (= Lemoniini Auctt.), and subdividing the broadly conceived tribe Nymphidiini into three subtribes, the monophyletic Nymphidiiti and Theopeiti Clench, 1955, and paraphyletic Lemoniaditi. A detailed phylogeny is generated for all 75 species in the Theopeiti utilising cladistic methodology to analyse 104 characters of behavioral ecology, wing pattern, genitalic and abdominal morphology for both sexes; the lemoniadit *Thisbe irenea* (Stoll, [1780]) was used as the outgroup. Five monophyletic clades are identified of generic status, three of which still require description, with *Archaeonympha* and "*Adelotypa*" *senta* (Hewitson, [1853]) being the most plesiomorphic and *Theope* the most derived. *Theope* is found to be divisible into 13, largely very well-supported monophyletic species groups, with the recognition of one miscellaneous polyphyletic species group deemed necessary; *Theope eurygonina* Bates, 1868, is found to be the most plesiomorphic species while members of the "*thestias*" and "*foliorum* groups" the most derived.

CHAPTER 1
INTRODUCTION

The family Riodinidae is unique among the butterflies in being almost exclusively confined to a single biogeographic region, the Neotropics, where approximately 1200 species or 95 percent of the familial diversity occurs, and where it constitutes about 20 percent of the total butterfly fauna (Robbins, 1982, 1993; Heppner, 1991; Robbins *et al.*, 1996). The Riodinidae is conspicuous not only for its species diversity but also for its great morphological and ecological diversity. Its biology is perhaps the most poorly known of any butterfly group, yet the study of riodinids promises to provide key insights into several aspects of evolutionary biology, including mimicry-driven phenotypic plasticity, mimicry being perhaps more rampant in this butterfly family than in any other (Bates, 1859; Seitz, 1916-20; D'Abrera, 1994; Miller, 1996), reproductive isolating mechanisms through highly species-specific male perching behaviors (Callaghan, 1983; Brévignon & Gallard, 1995; Hall, 1999), and myrmecophily and related topics of larval life history strategies (DeVries, 1988, 1990, 1991a,b,c, 1997). However, there are currently no detailed tribal, generic or species level phylogenies for the family upon which to trace major evolutionary adaptations and test competing hypotheses.

The first higher classification of the Riodinidae was attempted by Bates (1868), who created three subfamilies and several further divisions based solely on characters of wing venation, antennae and palpi. Not surprisingly, his classification was not followed by subsequent authors and it was not until the next century that Stichel (1910, 1911, 1928), using a broader range of external and internal characters, produced the first widely accepted classification, recognising two subfamilies and many tribal and subtribal divisions. The first attempt at a "modern", natural classification, based on monophyletic groups, was that of Harvey (1987), who recognized five subfamilies and eleven tribes for the Riodininae. Based on the most extensive examination of internal and external adult and early stage morphological characters to date, this classification has provided the platform needed from which to base more detailed systematic studies (Hall & Willmott, 1995a,b,c, 1996a,b,c, 1998a,b,c; DeVries & Hall, 1996; Brévignon & Gallard, 1997a,b, 1998a,b; Hall & Harvey, 1998; Hall, 1998a,b).

One of the aims of this work, using one of the largest morphological data sets ever compiled for the Lepidoptera, is to begin the process of recognising monophyletic groups in the Riodinidae below the tribal level and elucidating phylogenetic relationships between them, thus creating a natural generic classification and removing the main impediment to our understanding of character trait evolution in the group. The tribe of interest here is the Nymphidiini Bates, 1859 (*sensu* Harvey, 1987), perhaps the largest in the family (c. 200 species) (Hall, unpubl. data), and, exacerbated by its large number of very rare species, probably systematically the least understood of all the tribes (Harvey, 1987). As one of only three myrmecophilous tribes in the Riodinidae, along with the Eurybiini Reuter, 1897, and the Lemoniadini Kirby, 1871 (= Lemoniini Auctt. - see Hall and Heppner, 1999), studies in the Nymphidiini have provided a much deeper understanding of riodinid-ant symbioses and communication systems between caterpillars and ants (DeVries, 1990, 1991a,c, 1997; DeVries *et al.*, 1994). Harvey (1987) defined the tribe Nymphidiini on the basis of its members possessing a ventrally instead of dorsally positioned spiracle on male abdominal segment three and he placed it as the sister tribe to his Lemoniadini (as Lemoniini), on the basis of synapomorphies of larval morphology. However, to maintain the monophyly of the Nymphidiini, a few species need to be removed from the tribe as it is currently conceived (Bridges, 1994) and yet other species and even genera need to be included (Hall, in prep.). A few species treated by me in the Nymphidiini actually exhibit a medial spiracle position, but a consilience of other male genitalic characters affirms their tribal placement (Hall, in prep.) and the spiracular character forms a strong synapomorphy for the tribe.

I have examined the external facies of all species in the Nymphidiini, the male genitalia of approximately 85 percent of the species and the female genitalia of at least one species in each of the currently recognised genera, except the rare monotypic *Periplacis*. A preliminary cladistic analysis (Hall, in prep.), using a few wing pattern characters but predominantly male genitalic characters for the aforementioned 85 percent of species in the Nymphidiini, a representative from 8 out of the 10 currently recognised genera in the sister tribe Lemoniadini, and the morphologically similar *Pachythone conspersa* Sichel, 1926 (*incertae sedis* section [4 forewing radial veins] of Harvey, 1987) as an outgroup, produced a clear higher level pattern. These results suggest that the tribe Lemoniadini is paraphyletic with respect to the Nymphidiini, that the two should be merged, and that the Nymphidiini (*sensu strictu*) consists of two monophyletic clades. I thus propose the following subtribal structure for the newly conceived tribe Nymphidiini to facilitate communication about the group: Nymphidiiti for *Nymphidium*, *Calospila* and relatives, Theopeiti, the group studied here, for *Theope* and relatives, and Lemoniaditi (paraphyletic) for *Lemonias*, *Synargis* and relatives.

Penz & DeVries (in press), based on a cladistic analysis of 22 (31%) lemoniadine species and 9 (5%) nymphidiine species (*sensu* Harvey, 1987), with the unrelated *Stalachtis euterpe* (Stalachtini) as an outgroup, also concluded that the Lemoniadini and the Nymphidiini should be merged, but for what I believe are the wrong reasons, concluding that the Nymphidiini was paraphyletic with respect to the Lemoniadini, despite presenting no convincing synapomorphies for the latter tribe. We both agree, however, that the continued use of bifurcate "rami" (simply the eighth male sternite) as a character to define the Lemoniadini (after Harvey, 1987) is untenable. The inconsistency between the results of the two studies is surely explained in large part by the gross differences in taxon sampling and the concomitant changes in character recognition and coding, although choice of outgroup may also be important. The presence (Nymphidiiti) or absence (Theopeiti) of sclerotised tissue joining the distal portion of the valvae of the male genitalia (often termed a transtilla) characterises the monophyletic subtribes of the Nymphidiini; further male genitalic traits which contrast the subtribes and characterise the Theopeiti, include the lack of a vinculum dorsally, at the anterior edge of the tegumen, and the lack of a saccus.

This study specifically seeks to generate a comprehensive phylogeny for the subtribe Theopeiti, including all 75 member species, using cladistic methodology to analyse morphological characters, as a first step towards creating a phylogeny for the entire tribe (Hall, in prep.). In order to achieve this, it has been necessary to revise the largest constituent genus, *Theope* Doubleday, 1847, as it contained numerous undescribed species at the outset of revisional work; the taxonomy, biogeography and biology of this genus is discussed in detail, based on extensive museum research and fieldwork in Ecuador.

CHAPTER 2
A REVISION OF THE GENUS *THEOPE*: ITS SYSTEMATICS AND BIOLOGY (LEPIDOPTERA: RIODINIDAE: NYMPHIDIINI)

Introduction

The tribe Nymphidiini Bates, 1859 (*sensu* Harvey, 1987), is perhaps the largest in the Riodinidae Grote, 1895 (Hall, unpubl. data), and, exacerbated by the fact that it contains a great number of very rare species, the phylogenetic relationships among and taxonomic limits of its genera are equally the least understood of any tribe (Harvey, 1987). This last statement is amply true of *Theope* Doubleday, 1847, the largest genus in the tribe and also the third largest in the entire family, after the genera *Euselasia* Hübner, [1819], and *Mesosemia* Hübner, [1819] (Bridges, 1994; Hall, unpubl. data). Like most speciose riodinid genera, *Theope* contains many species that are very rare, many that are, at least superficially, very similar and difficult to identify (Hall, 1998a), and at the outset of revisionary work contained many undescribed species. It is for these reasons that, as part of a broader study to create a natural generic classification for the tribe Nymphidiini by means of comprehensive morphological cladistic analyses (Hall, in prep.), I decided to undertake a detailed revisional monograph of *Theope*, the first for any riodinid genus. Although a few reviews, either in part or in full, have been done for *Euselasia* (Stichel, 1928; Callaghan, 1997), *Methone* Doubleday, 1847 (Stichel, 1928), *Hades* Westwood, 1851 (Stichel, 1928), *Lasaia* Bates, 1868 (Clench, 1972), *Argyrogrammana* Strand, 1932 (Hall and Willmott, 1995a, 1996b), *Helicopis* Fabricius, 1807 (Stichel, 1928), *Sarota* Westwood, 1851 (Hall, 1998b), *Nymphidium* Fabricius, 1807 (Callaghan, 1985a,b, 1986b, 1988), and *Archaeonympha* Hall, 1998 (Hall and Harvey, 1998), none has been based on such an extensive review of worldwide museum material and literature, nor presented any original ecological information. Since *Theope* is such a large genus, I also take this opportunity to expand and utilise discussions on its ecology, particularly male perching behavior, and biogeography, to reach more broadly applicable conclusions for the Riodinidae as a whole.

Methods

This revision has been accomplished over a period of nearly six years, during which time I have observed and collected *Theope* individuals in the field, and examined specimens in a large number of institutions and private collections in Europe, North America and South America. Listed below are the acronyms, which largely follow Heppner and Lamas (1982) and Bridges (1994), for museum collections used throughout the text; specimens or, in the case of certain private collections, photographs, have been examined from all except those marked with an asterisk. Numbers in parentheses represent the number of *Theope* species held in the five most species-rich *Theope* collections, and include recently described species and those described here, whose types are imminently about to be deposited in the relevant collections.

AME	Allyn Museum of Entomology, Florida Museum of Natural History, Sarasota, FL, USA.
AMNH	American Museum of Natural History, New York, NY, USA
BMNH	(British) Natural History Museum, London, England (57)
DA	Collection of David Ahrenholz, St. Paul, MN, USA
DT	*Collection of David Trembath, London, England

ESM	Collection of Ernesto W. Schmidt-Mumm, Bogotá, Colombia
FSCA	Florida State Collection of Arthropods, Division of Plant Industry, Gainesville, FL, USA
GWB	Collection of George W. Busby, Boston, MA, USA
JHKW	Collection of Jason P. W. Hall and Keith R. Willmott, Gainesville, FL, USA (39)
JLC	Collection of Jean F. Le Crom, Bogotá, Colombia
JS	Collection of Julián A. Salazar E., Manizales, Colombia
JW	Collection of James J. Williams, Richmond, VA, USA
LC	Collection of Luis M. Constantino, Cali, Colombia
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA
MNHN	Musée Nationale d'Histore Naturelle, Paris, France (40)
MNCR	*Museo Nacional de Costa Rica, San José, Costa Rica
MUSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru
NSM	Nevada State Museum, Las Vegas, NV, USA
PJD	Collection of Philip J. DeVries, Eugene, OR, USA
QCAZ	*Quito Católica Zoología, Quito, Ecuador
RCB	Collection of Robert C. Busby, Boston, MA, USA
SA	Collection of Stéphane Attal, Paris, France
SMNS	*Staatliches Museum für Naturkunde, Stuttgart, Germany
UFP	*Departamento de Zoologia da Universidade Federal do Paraná, Curitiba, Brazil
UNAM	*Colección Entomológica de la Universidad Nacional Autónoma de Mexico, Mexico City, Mexico
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (52)

ZMHU Zoologische Museum für Naturkunde, Humboldt Universität, Berlin, Germany (42)

A total of 4243 *Theope* specimens were examined and identified in these collections, consisting of 2624 males, 1618 females (1:0.62 ratio), and a single gynandromorph (of *T. publius incompositus* Hall, n. subsp.). The extant primary types of all *Theope* species were examined except those of *T. villai* Beutelspacher, 1981 (UNAM, Mexico), *T. galionicus* Gallard & Brévignon, 1989 (in coll. of L. & C. Brévignon, Guadeloupe), and *T. amicitiae* Hall, Gallard & Brévignon, 1998 (recently deposited in MNHN), which have been identified on the basis of original illustrations of adults and male genitalia. All described taxa are illustrated here, including several species and sexes for the first time. To aid the identification process, an effort has been made to illustrate all specimens to approximately the same scale. Fifteen lectotypes are herein designated for the purposes of nomenclatural stability. These are designated in cases where male and female syntypes are not conspecific, where a female syntype can not be matched with the male syntype with absolute certainty because the female of one or more sibling species remains unknown or is currently unrecognised, and where a species is described from two type localities but labelled syntypes exist from only one of them, again leaving the possibility of a mixed type series.

Under the "Specimens Examined" section for each species are listed all the localities from which I have actually examined specimens (in a very few cases, photographs) together with the number of specimens examined from each locality and the collection in which they belong. Historical label data are used and it should be noted that two frequently listed Brazilian localities, Ega and Pará, are now referred to as Tefé (often also used here) and Belém respectively. Each locality is placed within a province/state for each country (except the island of Trinidad), but when this is not known, the locality is preceded by a question mark and placed at the end of the list for that country; if the country is not known, the question-marked locality is placed at the end of the entire list. If a specimen is labelled only with its province/state, it is entered under that region as "No specific locality data"; if only with its country of origin, it is entered under that country as "No locality data"; and if with no data at all, at the end of the entire list as "No locality data", following a full-stop. It is worth noting that historical BMNH specimens labelled "Ecuador, Río Napo" may in fact have originated from Loreto department in modern-day Peru but they remain listed under Napo province, Ecuador, for convenience; such data are never actually used to constitute a record for Ecuador, as all relevant species have been collected recently in that country by the author. Also, Nicaraguan specimens listed as originating from no specific locality in Chontales province were probably collected in the environs of Santo Domingo, in the north-eastern part of that province (Belt, 1874). Distributional data for the three species formerly included in *Parnes* Westwood, 1851 (see "Taxonomy" section), namely *nycteis* Westwood, 1851, *brevignoni* Gallard, 1996, and *philotes* Westwood, 1851, were not recorded in several of the above collections because it was not realised until later in the study that they belonged in *Theope*.

Given the paucity of capture dates for older specimens, which constitute the bulk of those examined, and the apparent year-round occurrence of most *Theope* species (see "Ecology" section), month of capture is only given for the rarest species, with the exception of largely field-collected Ecuadorian specimens, as a case study for seasonal distribution in a single country. Altitudinal specimen data, when available, are incorporated into the "Biology" section for that species. A small number of additional localities are included in the "Distribution" section that have been gleaned from reliable literature sources and, typically in the case of rare species or specimens providing interesting new distributional data, from personal communications. Detailed locality data listed under both the "Specimens Examined" and "Distribution" sections have been plotted onto maps of the Neotropics (Figs. 261-274), using a standard atlas, the NIMA GNS on-line gazetteer, and the Lepidoptera gazetteers of Brown (1979) (entire Neotropics), Lamas (1976) (Peru), and Brown (1941) (Ecuador). I was unable to locate a very small number of localities, predominantly those preceded by a question mark. For the sake of clarity, clusters of neighbouring localities for a given species are represented on the map with a single symbol, and when several species occur at the same locality, their symbols are somewhat spaced.

I carried out approximately twelve months of field work in Ecuador that was relevant to this project, visiting the wide variety of biogeographic zones, habitats and altitudes that exist in that country in which *Theope* species might be expected to occur, and *Theope* specimens were collected, and notes taken on various aspects of their ecology; along with notes also taken by K. R. Willmott in that country during eighteen months of often simultaneous field work, these form the basis of most of the introductory "Habitats and Ecology of Adults" section and the "Biology" sections for each species. Utilising the aforementioned Ecuadorian collection and loaned material from many of the above listed collections, male genitalia were dissected and are illustrated (Figs. 78-144), along with the taxonomically highly informative eighth tergite (Figs. 145-212) and sternite (see genitalia drawings), for all species except *T. villai*, as were female genitalia for approximately 70% of species. The remainder were either extremely rare and unavailable to me or simply unknown, as is the case for the majority of the "*foliorum* group". All of the male and female genitalic plates are drawn to the same scale except the last male genitalic plate, which is reduced by 20%, and the first female genitalic plate, which is enlarged by approximately 30%. For the female genitalic drawings (Figs. 213-260), stippled shading is implemented only for the ductus bursae and seminalis, to distinguish between sclerotised and non-sclerotised tissue; all the signae are heavily sclerotised, and only sclerotised portions of the ostium bursae are shown.

Dissections were performed using standard techniques, placing abdomens in hot 10% potassium hydroxide (KOH) for 10-20 minutes, and storing all material in glycerol after examination. Most illustrations were prepared using a Wild camera lucida attached to a Wild M4A stereomicroscope, but a few genitalic and external structures were also examined and are illustrated using a Hitachi S4000 digital scannning electron microscope (SEM); SEM examined structures were prepared by removing material from glycerol, rinsing it in water and air drying it before mounting it on stubs with carbon tape. I was often only able to dissect a single male specimen for the rarest species, but three or more male specimens per species were typically dissected for the more common ones to assess intraspecific genitalic variation, especially for sibling species when trying to establish defining genitalic characters. Some intraspecific variation was observed in the shape and size of certain structures of the male genitalia and eighth male tergite, and an effort is made here to illustrate typical specimens, with any such variation being discussed in the relevant species account. When available, a single female specimen was typically dissected per species, since in cases when more than one specimen was dissected, only slight intraspecific variation was observed. A list of all *Theope* dissections made, totalling 240 for both sexes, is given in Appendix B. The nomenclature for venation follows the widely used system of Comstock and Needham (1918), with cell spaces named after the vein above them (note that these are named after the vein below them in all my prior publications), and the terminology for male and female genital and abdominal structures follows Klots (1956) and Eliot (1973).

Taxonomy

Phylogenetic Placement

The most recent higher classification of the Riodinidae, which built on the earlier work of Bates (1868) and Stichel (1910-11, 1928, 1930-31), but incorporated a wider range of characters, including early stages, is that of Harvey (1987). He recognised five subfamilies and eleven tribes for the largest of these, the entirely Neotropical Riodininae, but the synonymy of the Sarotini Bridges, 1988 (= Charitini Auctt.) into the Helicopini Reuter, 1897, by Hall (1998b), and the downgrading of the tribe Lemoniadini (= Lemoniini Auctt. - see Hall & Heppner (1999)) to a subtribe of the Nymphidiini in this work, reduces the number of tribes to nine. The genus *Theope* was placed by Harvey (1987) in the largest of his riodinine tribes, the Nymphidiini, on the basis that the spiracle of male abdominal segment three (of larvae, pupae (see Fig. 7), and adults) was positioned ventrally instead of dorsally. With the exception of a few species whose spiracle is positioned medially, this is a strong synapomorphy supporting the monophyly of the group (Hall, in prep.).

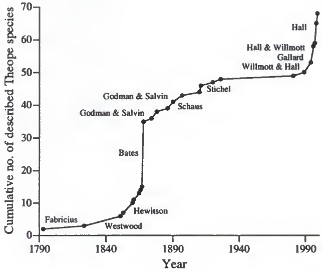
Theope can also be placed in the subtribe Theopeiti (**n. stat.**), erected by Clench (1955) as a full tribe with *T. eudocia* Westwood, 1851, as its type species. Since it was described on the basis of some spurious wing venation, leg and antennal characters that were reported to have been examined only in the type species, this family-group name has not been used by subsequent authors. However, I use the name here to refer to a monophyletic clade (subtribe) that includes *Theope*, *Archaeonympha* and three small undescribed genera. It is defined within the Nymphidiini (*sensu* Harvey, 1987) by not having the dorsal tips of the valvae of the male genitalia joined by sclerotised tissue. The remaining species in the Nymphidiini (*sensu* Harvey, 1987) may be placed in the subtribe

Nymphidiiti Bates, 1859, on the basis of possessing such sclerotised tissue. Other male genitalic characters typical of the Theopeiti, but present only in plesiomorphic members of the Nymphidiiti, include the possession of an incomplete vinculum dorsally and the lack of a saccus. It is enough to say here that the sister taxon to *Theope* appears to be "*Pandemos*" *godmanii* Dewitz, 1877, and that a detailed species-level phylogeny of the entire subtribe Theopeiti will shortly be presented elsewhere (Hall, in prep.; see Chapter 4). Although the monophyly of *Theope* + "*Pandemos*" *godmanii* is not supported by one or more universal morphological synapomorphies, a consilience of morphological characters does place them together as sister clades. An obvious behavioral ecological character that appears to be unique within the Theopeiti to these two clades is resting posture; member species rest with the wings folded over the body instead of spread open (DeVries, 1997, pers. comm.; M. Cock, pers. comm.; J.-Y. Gallard and C. Brévignon, pers. comm.; pers. obs.).

A History of Nomenclature

Many *Theope* species are somewhat reminiscent of lycaenids, perhaps especially those in the Australasian luciine genera *Philiris* Röber, 1891, and *Titea* Eliot, 1973, but very few of its members have ever been confused with other genera, and most of those rather atypical species that have, are only recognised as belonging to *Theope* in this work for the first time. The first *Theope* species were described by Fabricius in 1793 (see Fig. 1) in his omnibus genus *Hesperia*, but by the time Doubleday (1847) erected the genus *Theope* over fifty years later only one more species had been described, by Godart [1824] in the lycaenid genus *Polyommatus* Latreille, 1804. It is worth noting that the generic name *Theope* was redescribed ten years later by the prolific taxonomist Frederic Moore (Horsfield and Moore, 1858) for an Oriental satyrine butterfly, but as a junior homonym it

Fig. 1. A cumulative graph illustrating the number of *Theope* species described over time. All authors or authorship combinations that described two or more species in any given year are marked.



was replaced with the name *Ethope*. Westwood (1851) and Hewitson (1860) described a few species in the newly created riodinid genus, but it was not until the work of Henry Walter Bates (1868) was published, a product of twelve years' assiduous collecting in the then little explored Brazilian Amazon, that our knowledge of the genus became totally transformed with the description of an incredible twenty species. It is a testament to the uniformity and easily recognisable external features of *Theope* that these authors were readily able to describe their new species in that genus, as no type species was actually designated until Scudder (1875) did so, selecting *terambus* Godart, [1824], to be the type species. Around the turn of the century, four authors, Godman and Salvin (1878, 1886, 1897), Schaus (1890) and Stichel (1910, 1911, 1926) also made additional contributions to elucidating the diversity of *Theope*, particularly in Central America, and by the beginning of the twentieth century, the number of described *Theope* species had reached the upper forties, a number that remained constant and often cited until very recently (Seitz, 1920; Bridges, 1988, 1994; D'Abrera, 1994; DeVries, 1997).

For most butterfly groups, at the generic level or above, the pattern of cumulative species descriptions can be approximately described by an "S"-curve (e.g. see Ackery and Vane-Wright, 1984), but for a few mainly lycaenoid genera (but see Willmott *et al.*, in prep.), most of whose species are very rare, there is a "twist in the tail" or additional upturn in the description rate (see Fig. 1) that has occurred in the last two decades of the twentieth century and will continue into the beginning of the next. In the Riodinidae, *Theope* is one such genus, as are *Argyrogrammana* (Brévignon and Gallard, 1995, 1998c; Hall and Willmott, 1995a, 1996b, 1998a) and *Sarota* (Brévignon and Gallard, 1998a; Hall, 1998b). Largely as a result of recent intensive field work, especially in Ecuador, Peru, Brazil, and French Guiana, many more new *Theope* species have been discovered, mainly in the "*pedias*", "*sericea*" and "*foliorum* groups" (Gallard and Brévignon, 1989; D'Abrera, 1994; Willmott and Hall, 1994; Hall and Willmott, 1996; Gallard, 1996; DeVries and Hall, 1996; Hall and Austin, 1997; Hall, 1998a); as a result of my field work in Ecuador, six undescribed *Theope* species were discovered, including two that remain known only from Ecuador. The inclusion of two new species described in this work and five species newly brought into combination with *Theope*, and the exclusion of two further species (see below), brings the current species total for the genus to sixty-eight. However, the fact that a number of *Theope* species are known from only one or a handful of specimens is a sure indicator that a few species still remain to be discovered, perhaps in the Chocó or in poorly collected areas around the edges of the Amazon basin. In fact, I have examined a photograph of a single female *Theope* that appears to be an undescribed species in the "*hypoleuca*" or "*foliorum* group" (E. Furtado, pers. comm.) from Mato Grosso, south-west Brazil, and it may be this species that Brown (1987), in a list of Mato Grosso butterflies, refers to as "*Theope* sp. nov.". The description of this particular species, if closer examination indicates that it is indeed new, must await the discovery of male specimens.

Five described species are treated here in *Theope* for the first time and this necessitates the synonymy of two genera. The first of these species, *antanitis* Hewitson, 1874, was described in *Lemonias* Hübner, [1807], and subsequently treated in *Polystichtis* Hübner, [1819], and *Calospila* Geyer, [1832] (Stichel, 1911, 1930; Seitz, 1920; Bridges, 1994), but dissection of the unique syntype and examination of its male genitalia reveal it to be the sister species to *T. sisemina* Seitz, 1920. The second species, *orphana*, was described by Stichel (1911) as the type species of his new genus *Dinoplotis*, on the basis that forewing vein R1 was entirely fused with vein Sc except at its base. The use of wing venation characters in Lepidoptera classification has had a long history (Herrich-Schäffer, 1843-56; Comstock & Needham, 1918; Miller, 1970a; Heppner, 1998), however, I have found them to be highly homoplasious at low taxonomic levels in the Riodinidae, and this character state reoccurs in the distantly related *T. guillaumei* Gallard, 1996. Indeed a whole range of intermediate states of fusion exist between these two veins in the genus *Theope* (see Figs. 2a-e). This same wing venation character was also found to be homoplasious by Miller (1987) within genera of the Papilionidae. These are surely cautionary tales for the use of such minor wing venation characters in constructing riodinid classifications, and an exactly analogous situation in the *incertae sedis* section (5 FRV) of Harvey (1987) suggests that the genus *Cremna* Doubleday, 1847, is very dubiously separated from *Napaea* Hübner, [1819]. Scott (1983) even presents evidence that flight behavior can affect wing shape and thus the position of forewing radial veins, an ecological character that can certainly vary between closely related species. *T. tetrastigma* Bates, 1868, is one of the *Theope* species that has forewing veins R1 and Sc fused for a considerable distance and, in fact, dissection of the holotype of *orphana* and examination of its male genitalia indicate that it is the sister species to *T. tetrastigma*. Thus *Dinoplotis* becomes a synonym of *Theope*. Finally, cladistic analyses (presented elsewhere (Hall, in prep.)) indicate that the three species formerly included in *Parnes*, namely *nycteis*, *brevignoni*, and *philotes*, form a sister clade to *tetrastigma* + *orphana*, and I thus also treat *Parnes* as a synonym of *Theope*. The highly atypical and striking "ripple" wing pattern (see Nijhout, 1991) of *T. nycteis* and *T. brevignoni*, appears to be an ecological adaptation to living in the gloomy forest understory.

The only removal of species from *Theope* was done recently, also as a result of my revisionary work. The taxon *drepana* Bates, 1868, was described in *Theope*, no doubt because of its small size and unusual possession of blue dorsal coloration, and its systematic position was never questioned by subsequent authors until recently (Lamas, 1994; Hall and Willmott, 1996c), despite the fact that a synonym of it, *sinuata* Stichel, 1925, was concurrently being treated in another genus of superficially similar species, *Comphotis* Stichel, 1910 (see Hall and Willmott, 1996c). It is thus not surprising that its sister species, *urichi* Vane-Wright, 1994, was also described in *Theope* (in D'Abrera, 1994). However, both these species lack the wing pattern synapomorphy for *Theope* (see below), and *drepana* also lacks the male abdominal synapomorphy (see below) (the male of *urichi* is unknown), although the male genitalic morphology of *drepana* does place it, and hence its sister species, within the subtribe Theopeiti. The aforementioned morphological cladistic analyses (Hall, in prep.) confirm that these species do not belong in *Theope*, as conceived here, and indicate that they do not form a sister group to *Theope* (i.e. together forming a monophyletic group). To maintain the monophyly of *Theope*, a new genus, *Archaeonympha*, was described to include the taxa *drepana*, *sinuata* and *urichi*, and a newly described species, *smalli* Hall & Harvey, 1998 (Hall and Harvey, 1998).

Characteristics of *Theope*

By virtue of their small size (average forewing length approximately 14mm), often uniform coloration and apparently minimal number of external diagnostic features, many *Theope* species can appear confusingly similar. This great interspecific similarity and their propensity for intraspecific geographic variation has always created difficulties in identification and led Seitz (1920) to the largely incorrect assumption that many were only "deviations of the flying place". With few exceptions (e.g. *T. comosa* and *T. janus*), *Theope* species are sexually monomorphic and females typically only have more rounded wings than males and paler coloration; with fewer and less variable genitalic characters, the females of some sister species pairs (e.g. *T. eudocia* and *T. acosma*) are almost inseparable. The majority of species have varying shades and patterns of blue on the dorsal surface, but exceptionally this is brown, white or orange. The males of certain species, particularly in the "*sericea*" and "*terambus* groups", additionally possess an area of pale brown postdiscal scaling on the dorsal forewing. The physiological function of many scale types is still very uncertain (Downey and Allyn, 1975; Scoble, 1991), and, although under a SEM microscope no modifications for pheremonal dissemination can be seen (Fig. 3c), I tentatively conclude that they must represent androconial scales.

The ventral wing surface is typically a monochrome gray, brown, white or pale to golden chrome yellow, although many species possess submarginal black spots, occasionally surrounded by white or bluish-white, and a few possess a variable number of transverse brown bands. The males of a few species in the "*sericea*" (e.g. *T. galionicus*) and "*theritas* groups" (e.g. *T. comosa*) have long, piliform, presumably androconial hairs at the anal margin of the ventral forewing (Fig. 3d), and the presence of these is typically

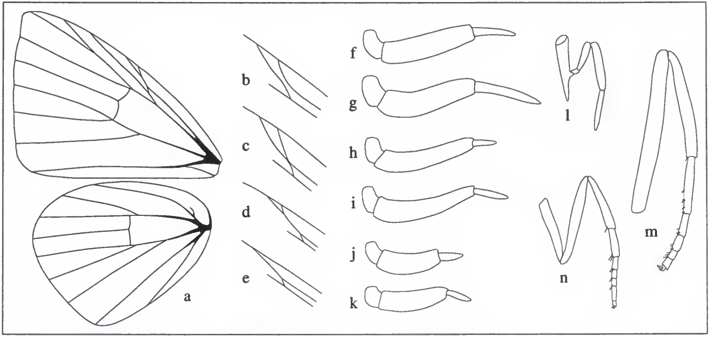
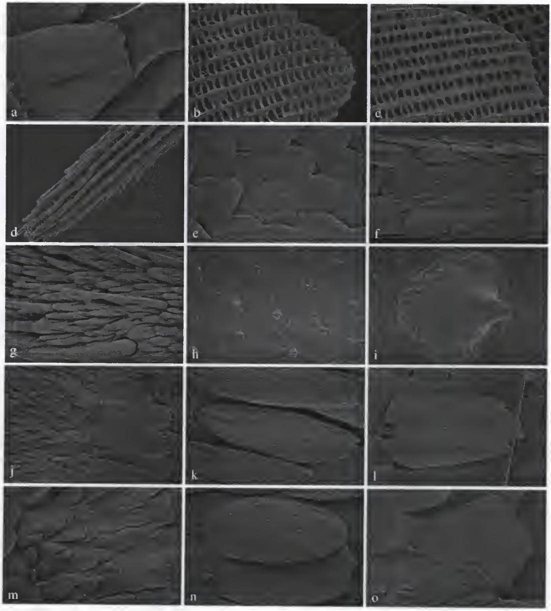


Fig. 2.2. *Theope* morphology. Male venation (FW radial veins only for b-e): a) *T. tetrastigma*; b) *T. archimedes*; c) *T. decorata*; d) *T. philotes*; e) *T. orphana*. Palpi: f) male *T. pedias*; g) female *T. pedias*; h) male *T. barea*; i) female *T. barea*; j) male *T. decorata*; k) female *T. decorata*. Legs of *T. lycaenina*: l) male foreleg; m) male midleg; n) female foreleg.

Fig. 2.3. Scanning Electron Micrographs (SEM's) of *Theope* morphology: a) blue DFW scales of *T. aureonitens* (x 1100); b) a single blue DFW scale of *T. aureonitens* (x 11,000); c) a single pale brown postdiscal DFW scale of *T. aureonitens* (x 11,000); d) a seta from anal margin of VFW of *T. sobrina* (x 15,000); e) flattened scales at costal margin of DHW of *T. sobrina* (x 600); f) the inner edge of a nudum antennal segment of *T. lycaenina* (x 500); g) a magnified section of "f" showing three types of antennal sensory setae (x 3500); h) internal view of corpus bursae wall of female genitalia of *T. eupolis* illustrating anteriorly directed spines (x 1500); i) a single magnified spine from "h" (x 18,000); j) dorsal view of male abdominal segment three of *T. eudocia* highlighting boundary between two different scale types (x 400); k) a normal abdominal scale from "j" (x 1500); l) the smaller, modified scales from "j" (x 3000); m) dorsal view of male abdominal segment three of *T. sobrina* at boundary between two different scale types (x 450); n) the normal abdominal scales from "m" (x 1100); o) the smaller, modified scales from "m" (x 2000).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correlated with a bare, often paler brown patch of more rounded and flattened scales at the costal margin of the dorsal hindwing (Fig. 3e) against which they rub. A universal wing pattern synapomorphy for *Theope* is the total absence of any spots or rare presence of a single spot (e.g. *T. eurygonina*) instead of two at the base of cell Cu2 on the ventral forewing. Such a loss/reduction does also occur in the Nymphidiiti genera *Setabis* Westwood, 1851, *Pandemos* Hübner, [1819], and *Zelotaea* Bates, 1868, but the completely uniform, patternless ventral surface seen in many *Theope* species is unique to the genus. As discussed above, the extent of fusion of the basal forewing radial veins is interspecifically very variable but the length of vein R3 and the exact position that vein R4 touches the apex are similarly so.

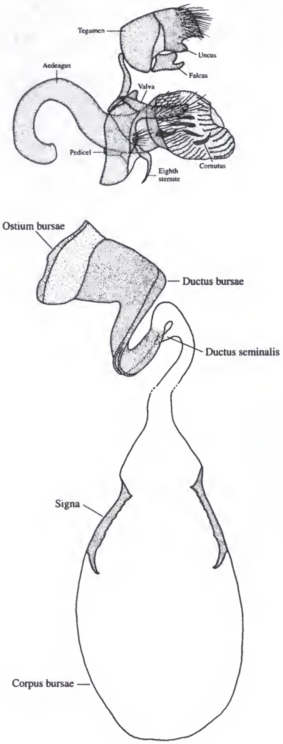
The eyes of *Theope* species are bare, and the frons typically has a brown medial band and paler brown, white or yellow at the margins and surrounding the eyes. The antennal segments are black with white scaling at the base ventrally, and vary in number from 35 (*nycteis*) to 59 (*excelsa*), a character that I have found approximately correlates with forewing length. No significant sexual dimorphism is apparent in these characters, but, as noted by Forbes (1958) and Robbins (1991) for the Lycaenidae, the extent of the nudum area (region devoid of scaling along the inner edge of each segment) is typically slightly greater in females, presumably correlating with the oviposition behavior of myrmecophilous species (see the "Morphology and Ecology of Immature Stages" section); under a SEM, three types of sensory setae are visible on such nudum segments (see Figs. 3f,g). The clubs are typically tubular and black, with orange tips. The second palpal segment is variably long, as it is in all genera of the Nymphidiini, and the third segment varies continuously from short, in the "*sericea* group", to very long, in the "*archimedes*", "*pedias*" and "*eudocia* groups" (Figs. 2f-k); the upper surface is typically black while the ventral surface mirrors that of the ventral wing coloration.

As is typical of fast flying, territorial butterflies (see "Ecology" section), the thorax is robust, and the medium length abdomen is of roughly the same width; both are usually black dorsally, although also occasionally blue or orange-brown, and usually reflect the ventral wing coloration ventrally. The males of most species of the "*pedias*" and "*eudocia* groups", and a few in the "*theritas* group", possess a distinct patch of smaller, modified dorsal scales on certain medial abdominal segments (Figs. 3j-o) that are probably androconial in function . The legs are unremarkable, the foreleg of the male having a unimerous tibia without any ventral spines, and the mid and hindlegs having a single tibial spur and clusters of spines on the tibial segments in all of the five phylogenetically disparate species examined (Figs. 2l-n).

The last abdominal sclerites of male *Theope* species are modified to an extraordinary extent that is not seen elsewhere in the Riodinidae. Such structures have been demonstrated to aid in clasping the female abdomen during copulation in josiine moths (Miller, 1988, 1996), and not surprisingly they show considerable interspecific variation, thus providing excellent taxonomic and phylogenetic information. The species of several groups have variably sized and shaped projections from the lower posterior corner of the eighth tergite, with variably broad sclerotised invaginations of the distal margin, and those of the "*thestias*" and "*foliorum* groups" have a fenestration of presumably spiracular origin in the middle of the eighth tergite, a character that provides strong evidence for the monophyly of these two derived groups. *Theope* species are unique in exhibiting a wide variety of often bizzare-looking, three-dimensional modifications to the last male sternite, and their shape and extent of ventral reduction provide some of the best specific characters and species-group level synapomorphies. Indeed, a continuous, well-sclerotised invagination that joins the distal portion of the eighth sternite to the genital armature is the only unique, universal synapomorphy for *Theope*. Since the two structures are typically attached when dissected, the eighth sternite is illustrated here for all species *in situ* in this position. The last tergite of females exhibits a variably sclerotised disc at the upper posterior corner that is also variably elongate in certain "*theritas* group" species, and these characters are of some limited taxonomic value.

The male genitalia of *Theope* species (see Fig. 4) provide a wealth of charactes for delimiting species groups and separating otherwise superficially very similar species, for example those in the "*foliorum* group". The tegumen of the male genitalia is typically a broad triangle, connected to the uncus by a triangular lateral fenestration. The uncus is essentially rectangular with a variably concave distal margin that is often produced into one or two points at the lower posterior corner; the upper distal portion has a variably large lightly sclerotised region and this is where the majority of setae are concentrated. The vinculum is a thin ribbon that is unusual in being not present along the entire length of the anterior margin of the tegumen (i.e. incomplete) (see "Phylogenetic Placement" section); medial and upper posterior projections of varying lengths, similar to those of certain species in the symmachiine genus *Pirascca* Hall and Willmott, 1996 (see Hall and Willmott, 1996c), are present in a few *Theope* species groups but not seen in any other nymphidiine genera and, again unusually in the tribe, no species has a true anteriorly-pointing saccus ventrally. The shape and size of the valvae are more interspecifically variable in *Theope* than in any other nymphidiine genus and each species group tends to be well diagnosed by their form. The valvae of most species have a basal lateral bulge but the remainder may be a simple rectangle or highly modified into long upper or lower posterior projections; the anterior portion is fused for a variable distance with the vinculum, but, as noted earlier, the valvae are not fused towards their tip, as in all members of the Nymphidiiti. The aedeagus is generally long and thin, although it may be downwardly or

Fig. 4. Typical male (above) and female (below) *Theope* genitalia (*T. wallacei*), highlighting structures discussed throughout the text.



upwardly pointed towards the posterior tip, where it typically opens dorsally, and in a few species groups it is highly contorted anteriorly; the pedicel is short, generally very well sclerotised and sometimes laterally thickened. Most species have only tiny sclerotised sculpturing on the aedeagal vesica, but well-defined scobinate patches and variably sized cornuti do occur in a few species, most notably those of the "*sericea*", "*terambus*" and "*foliorum* groups" .

Female genitalia (see Fig. 4) have been utilised relatively little in Lepidopteran systematics compared to those of the male, and they were not integrated into a unified classification of the Riodinidae until the work of Harvey (1987). This study represents the most extensive review of female genitalia in any single large group of the Riodinidae. The corpus bursae of the female genitalia in *Theope* is generally elongate and rounded and, at least in the two species examined under a SEM microscope, has variably sized and spaced, anteriorly directed spines on its inner surface (Figs. 3h,i). Such structures are reported by Robbins (1991) for the eumaeine lycaenid genus *Rekoa* Kaye, 1904, and are presumably widespread but unstudied in the Lepidoptera. All species except *T. eurygonina* have a pair of sclerotised and invaginated signae that vary sufficiently in shape interspecifically as to provide good species group characters; they may be simple semicircles or rectangles, or form a long inwardly directed spine, and they generally have an ovoid opening to the corpus wall. Both the signae and the smaller internal spines are thought to aid in positioning the spermatophore (Robbins, 1991). The ductus bursae is typically very long and broadest posteriorly, where it may become variably sclerotised and even also highly coiled in certain "*foliorum* group" species, a character not reported elsewhere in the family; the ductus seminalis joins the ductus bursae at a variety of posterior positions and exhibits some sclerotised sculpturing only in species of the "*pedias*" and "*eudocia* groups". The ostium bursae may form an entirely sclerotised ring or be sclerotised only ventrally, and in a few species has lateral or dorso-lateral projections.

As mentioned previously, a cladistic analysis of the Theopeiti has been completed using some of the aforementioned external and internal morphological characters and many more (Hall, in prep.), and the resultant phylogeny is reflected in the classification and sequence in which the species are treated in this revision, which begins with the most plesiomorphic species and finishes with the most derived. I here recognise fourteen species groups, the members of which are outlined later in Tables 2 and 5, which are all named after the earliest described component species. All are hypothesised to be natural groups, selected on the basis of monophyly, except one polyphyletic "miscellaneous" group that contains four divergent species belonging to none of the well defined groups. I treat these species in one group instead of four for the sake of convenience and in the belief that, by definition, a single species can not constitute a group and be the focus of generalisations. The only other subjective decision made in delineating species groups concerns the "*sericea* group", which consists of two distinct monophyletic clades, as externally defined by the possession of a pale or golden chrome yellow ventral surface; however, on the basis that the morphology and ecology of the component species in these clades are insufficiently different to warrant their separation, I prefer to retain a single, more inclusive group. The synapomorphic and other distinctive characters of each species group are given in Table 1. All of these groups are well defined and strongly supported, with the exception of the "*hypoleuca* group", whose monophyly is uncertain.

Table 2.1. A list of synapomorphic characters and other characteristic features for each species group in *Theope*. Numbers in square brackets indicate the number of species in each group. Abbreviations: M = male; F = female; DS = dorsal surface; VS = ventral surface; DFW, DHW = dorsal forewing/ hindwing; VFW, VHW = ventral forewing/ hindwing.

	Group						
Characters	**I *nycteis* [3]**	**II *tetrastigma* [2]**	**III *hypoleuca* [3]**	**IV *archimedes* [2]**	**V *pedias* [4]**	**VI *eudocia* [2]**	**VII *sericea* [9]**
Synapomorphies:							
Wing pattern	submarginal spots on VHW enlarged in apex	None	None	red scaling at base of VFW	None	DS predominantly orange	None
Abdomen and genitalia	last M sternite long & thin with no lateral projections	M genitalia: lightly scl. lateral tissue towards tip of aedeagus; a single, elongate, narrow cornutus in aedeagus	None	thin, contrasted whitish line along VS of abdomen. M genitalia: lower portion of uncus a broadly elongate triangle; valvae evenly elongate & rounded at tip. F genitalia: dorsal portion of ostium bursae reduced to scl. triangle in each corner	None	M genitalia: valvae rectangular with a single posteriorly projecting point from middle of distal edge	F genitalia: signae large and "horn"-shaped
Other characteristic features:	males perch during morning and afternoon; fly low to ground around tree trunk bases; small size; brown DS; fine yellow "ripple pattern" on VS; thin yellow line at distal margin of VS; submarginal spots on VS black with white pupils; & restricted to apex on VFW; M genitalia: uncus rectangular without modification at distal margin	exclusively Amazonian; males perch late in afternoon; small size; brown DS; thin yellow line at distal margin of VS; last M tergite has a sharply indented ventral margin anteriorly; M genitalia: valvae upwardly pointed with pointed lower projection	exclusively Amazonian; small size; VS pale, only plesiomorphic group with no submarginal spots on VS; M genitalia: variety of internal scl. aedeagal structures	large size; palpi elongate; darkly outlined venation on VS; contrasted postdiscal and submarginal whitish scaling on VS	occur in forest edge and riverside habitats; palpi elongate; patch of smaller, paler scales on DS of M abdominal segment 3; HW elliptical; elongate postdiscal blue that includes cell Cu_1 on DFW of F; VS dark yellow/ orange; M genitalia: tegumen narrow; valvae rectangular; F genitalia: ductus seminalis hardened with studded sculpturing	males perch during morning and afternoon; & for relatively long time; palpi elongate; patch of smaller, paler scales on DS of M abdominal segment 3; HW elliptical; VS pale yellow; M genitalia: lower portion of uncus produced into two small points; aedeagal tip opens to right; F genitalia: ductus seminalis hardened with studded sculpturing	males almost exclusively found perching on hilltops; & for relatively short time; postdiscal area of pale brown scaling on DFW; all ventral body parts yellow; VS pale/ chrome yellow; last M sternite large; M genitalia: lower portion of uncus produced into two small points; vinculum forms ventral, anterior "bulb"; wide variety of scl. aedeagal structures; pedicel laterally thickened

Table 2.1. Cont….

				Group			
Characters	**VIII Miscellan. [4]**	**IX *antanitis* [2]**	**X *virgilius* [4]**	**XI *terambus* [7]**	**XII *theritas* [8]**	**XIII *thestias* [5]**	**XIV *foliorum* [13]**
Synapomorphies:							
Wing shape and pattern	None (polyphyletic group)	medial white band on both ventral surfaces	None	None	FW costa strongly bowed; elongate postdiscal blue in cells M_3 & M_2 only on DFW in F	prominent yellow scaling at base of VFW	None
Abdomen and genitalia	None (polyphyletic group)	M genitalia: valvae narrow with basal lateral bulge of same length	last M sternite "born"-shaped. M genitalia: "hump"-like posterior projection from medial region of vinculum	M genitalia: elongate triangular posterior projection from medial region of vinculum; single arrow-shaped aedeagal cornutus; F genitalia: ostium bursae laterally elongate & shaped like an "open mouth"; signae elongate & rounded	last M sternite asymmetrical; & dorsal portion produced into one or two long, dorso-lateral projections. M genitalia: lower portion of uncus triangular & downturned; falci angularly rectangular at base (<90°), straight & rounded; elongate posterior projection from upper portion of vinculum; pedicel asymmetrical	last M sternite reduced to vestigial band. M genitalia: lower portion of uncus a narrowly elongate triangle; vinculum forms a ventral, posterior "cup"; valvae narrow and twisted. F genitalia: ostium bursae has posteriorly concave, triangular lateral flanges	M genitalia: vinculum incomplete, extending from tegumen to top of valvae; valvae have an upper posterior projection or "arm"
Other characteristic features:	None (polyphyletic group)	probably exclusively inhabit Andean cloud forests; DS partially white; last M tergite has small posterior projections; last M sternite has long dorso-lateral projections; M genitalia: aedeagus long, thin & upwardly pointed; lower portion of uncus produced into two small points	blue scaling on DS of thorax and abdomen; isolated subapical blue patch on DFW of F; submarginal spots on VS surrounded by bluish-white scaling; last M tergite has large rounded projections; M genitalia: small anterior region on dorsum of uncus devoid of setae; valvae rectangular & tilted over aedeagus; abrupt upturned tip to aedeagus; scl. plate inside aedeagus; F genitalia: ventral portion of ostium bursae an angular "U" shape; signae elongate at base, serrate along inner edge, sharply downwardly pointed at tip	large size; postdiscal area of pale brown scaling on DFW; isolated subapical blue patch on DFW of F; dark brown transverse band on each ventral wing; submarginal spots on VS surrounded by bluish-white scaling; last M tergite has small posterior projections; M genitalia: small anterior region on dorsum of uncus devoid of setae; valvae rectangular & tilted over aedeagus; abrupt upturned tip to aedeagus; scl. plate inside aedeagus;	almost exclusively Amazonian; males perch early in afternoon; most species externally very similar; HW elliptical; area of pale brown scaling at costa of DHW in M; VS shades of brown; last M tergite has large, asymmetrical posterior projections; & a broad scl. invagination at distal margin; & a markedly angular anterior margin; M genitalia: tegumen elongate; vinculum projection asymmetrical; valvae bifurcate with a basal lateral bulge and a medial posterior projection; anterior portion of aedeagus contorted; F genitalia: signae sharply pointed	occur in 2° & forest edge habitats; female biased sex ratio; small size; last M tergite contains tiny fenestration; & has small posterior projections; purple iridescence on VS; large anal fold on HW; M genitalia: falci angularly rectangular at base (>90°), remainder upwardly pointed; last F tergite dorso-ventrally elongate; F genitalia: signae rounded with a concave distal margin	contains many v. rare species; subtle yellow tinge along costa of VFW; dark line at very distal margin of VS; last M tergite contains tiny fenestration; & anterior margin is markedly angular; M genitalia: uncus has rounded or downwardly pointed upper posterior projection; falci angularly rectangular at base (<90°), straight & pointed; anterior portion of aedeagus contorted; & posterior portion evenly, upwardly pointed; one or more tear-drop shaped internal aedeagal cornuti; F genitalia: posterior portion of ductus bursae scl. & coiled

Proposed Classification of *Theope*

Presented below is a synonymic checklist of all species treated as belonging to *Theope* in this work. I use Bridges (1994) as a reference upon which to base my nomenclatural changes, marked in bold type, and take into account the few subsequently, explicity stated nomenclatural changes of D'Abrera (1994) and DeVries (1997). A single dash, "-", refers to a subspecies, and a double dash, "--", refers to a synonym; "n. stat." indicates a previously unrecognised status for a taxon; "stat. rev." indicates a reversal to a previously recognised status for a taxon; "n. syn." indicates a previously unrecognised synonymy of a taxon; "n. comb." indicates a previously unrecognised generic combination for a taxon; "repl. n." indicates a replacement name for a taxon due to homonymy, and "H" indicates a homonym.

Theope Doubleday, 1847 (68 species)
acosma Stichel, 1910 **n. stat.**
amicitiae Hall, Gallard & Brévignon, 1998
antanitis (Hewitson, 1874) **n. comb.**
apheles Bates, 1868
archimedes (Fabricius, 1793)
-- *thebais* Hewitson, 1860 **n. syn.**
- *zyzyxoxyx* D'Abrera, 1994 **n. stat.**
atima Bates, 1868
aureonitens Bates, 1868
azurea Bates, 1868
bacenis Schaus, 1890
-- *mania* Godman & Salvin, 1897 **n. syn.**
-- *eleutho* Godman & Salvin, 1897 **n. syn.**
barea Godman & Salvin, 1878
-- *caenina* Godman & Salvin, 1878
basilea Bates, 1866
batesi Hall, 1998
brevignoni (Gallard, 1996) **n. comb.**
busbyi Hall, 1998
comosa Stichel, 1911
cratylus Godman & Salvin, 1886
dabrerai Hall & Willmott, 1996
decorata Godman & Salvin, 1878 **stat. rev.**
devriesi Hall & Willmott, 1996
discus Bates, 1868 **stat. rev.**
eudocia Westwood, 1851
-- *pulchralis* Stichel, 1910 **n. syn.**
eupolis Schaus, 1890
-- *diores* Godman & Salvin, 1897 **n. syn.**
-- *talna* Godman & Salvin, 1897 **n. syn.**
eurygonina Bates, 1868
-- *columbiana* Staudinger, 1888 **n. syn.**
excelsa Bates, 1868
foliorum Bates, 1868
-- *punctipennis* Bates, 1868
-- *herta* Godman & Salvin, 1886 **n. syn.**
galionicus Gallard & Brévignon, 1989
christiani Hall & Willmott **repl. n.**
-- *brevignoni* Hall & Willmott, 1996 **H**
guillaumei Gallard, 1996
- *cecropia* DeVries & Hall, 1996
hypoleuca Bates, 1868
iani Willmott & Hall, 1994
janus Bates, 1867
kingi Hall & Willmott, 1996
lampropteryx Bates, 1868
leucanthe Bates, 1868
lycaenina Bates, 1868
matuta Godman & Salvin, 1897 **stat. rev.**
- *heureka* Hall **n. subsp.**
methemona Bates, 1868
mundula Stichel, 1926
nobilis Bates, 1868 **n. stat.**
nodosus Hall **n. sp.**
nycteis (Westwood, 1851) **n. comb.**

orphana (Stichel, 1911) **n. comb.**
pakitza Hall & Harvey, 1998
pedias Herrich-Schäffer, [1853]
-- *thelpusa* Hewitson, 1860
-- *hypoxanthe* Bates, 1868
-- *isia* Godman & Salvin, 1878 **n. syn.**
pepo Willmott & Hall, 1994
phaeo Prittwitz, 1865
-- *theutis* Godman & Salvin, 1886 **n. syn.**
-- *folia* Godman & Salvin, 1886 **n. syn.**
philotes (Westwood, 1851) **n. comb.**
pieridoides C. & R. Felder, 1865
-- *bahlmanni* Fassl, 1922 **n. syn.**
pseudopedias Hall **n. sp.**
publius C. & R. Felder, 1861
- *incompositus* Hall **n. subsp.**
sanjuani D'Abrera, 1994
sericea Bates, 1868
simplicia Bates, 1868
sisemina Seitz, 1920
- *tabacona* Hall & Willmott, 1996
sobrina Bates, 1868
speciosa Godman & Salvin, 1897
-- *fasciata* Lathy, 1904
-- *phineus* Schaus, 1913
sticheli Hall, 1998
syngenes Bates, 1868
terambus (Godart, [1824])
-- *lytaea* (Geyer, 1837)
tetrastigma Bates, 1868
theritas Hewitson, 1860
thestias Hewitson, 1860
thootes Hewitson, 1860
turneri Hall & Austin, 1997
villai Beutelspacher, 1981
virgilius (Fabricius, 1793)
-- *caerulea* Bates, 1868 **n. syn.**
-- *polimela* Godman & Salvin, 1897 **n. syn.**
wallacei Hall, 1998
zostera Bates, 1868

A key to the Adult Males of *Theope*

To make the presented key usable in the field, all couplets are based on visually obvious external characters. Although the sexes of many species are not dimorphic, and the females of those species will successfully key out, the dimorphism of others makes an integrated key for both sexes impossible. Since the females of many species are not known, and a few of those that are can be virtually indistinguishable from each other, it was not deemed practical to construct a key for females, and these must be identified solely from the illustrations and identification notes in each species account. Due to variation in the prominence of ventral submarginal spots in *T. thootes*, *T. lycaenina* and *T. wallacei*, it was necessary to key each of these species out twice, and because of the large wing pattern differences between the two subspecies of *T. sisemina*, they are each keyed out separately. Here and throughout the rest of the text, I use the following abbreviations: DFW/DHW = dorsal forewing/ hindwing; VFW/VHW = ventral forewing/ hindwing.

1. Dorsal surface with blue, white or orange pattern elements 7
Dorsal surface entirely brown 2
2(1). Yellow along base of VFW absent 3
Yellow along base of VFW present ....*guillaumei*

3(2). A fine-grained, yellow-banded ventral "ripple" pattern absent 5
A fine-grained, yellow-banded ventral "ripple" pattern present 4
4(3). White pupils in black apical spot of VHW positioned centrally ....*nycteis*
White pupils in black apical spot of VHW positioned proximally ......*brevignoni*
5(3). Submarginal spots on VFW restricted to or enlarged in apex 6
Submarginal spots on VFW evenly distributed around entire margin ..*tetrastigma*
6(5). Submarginal spots on VFW greatly enlarged in apex ....*philotes*
Submarginal spots on VFW evenly distributed around entire margin ......*orphana*
7(1). Dorsal surface with blue or orange pattern elements 10
Dorsal surface with white pattern elements on both wings 8
8(7). DHW entirely white 9
White on DHW restricted to a variably broad medial band ......*sisemina sisemina*
9(8). White on DFW occupies entire basal two-thirds of wing ....*pieridoides*
White on DFW a broad band that is absent from discal cell ....*antanitis*
10(7). Red at very base of VFW absent 12
Red at very base of VFW present 11
11(10). Red at very base of VFW faint, average forewing length 16mm, blue in DFW cell 1A+2A extends further distally than that in cell below ....*archimedes*
Red at very base of VFW prominent, average forewing length 17.5mm, blue in DFW cell 1A+2A extends as far or less far distally than that in cell below .*matuta*
12.(10) Ventral ground color shades of brown, gray or white 29
Ventral ground color shades of yellow or orange 13
13(12). Ventral ground color shades of yellow 15
Ventral ground color orange and margins of ventral surface with brown scaling14
14(13). Purple-blue squares at distal margin of DFW absent, dorsal blue unicolorous ....*devriesi*
Purple-blue squares at distal margin of DFW present, dorsal coloration a mixture of blue and purple ....*pepo*
15(13). Ventral ground color shades of matte yellow..........20
Ventral ground color golden chrome yellow 16

16(15). A large area of prominent pale brown postdiscal scaling on DFW absent 17
A large area of prominent pale brown postdiscal scaling on DFW present ....***aureonitens***

17(16). Blue on DFW an approximate semicircle 18
Blue on DFW restricted to anal margin ....***lampropteryx***

18(17). Hairs along anal margin of VFW short or absent 19
Hairs along anal margin of VFW long ....***galionicus***

19(18). Cell Rs of DFW with no blue or only a few blue scales at base..........***sericea***
Cell Rs of DFW entirely blue ....***dabrerai***

20(15). Dorsal surface predominantly blue 22
Dorsal surface predominantly orange 21

21(20). A subapical blue patch on DFW absent ....***acosma***
A subapical blue patch on DFW present ....***eudocia***

22(20). A small area of contrasted paler brown postdiscal scaling on DFW absent 25
A small area of contrasted paler brown postdiscal scaling on DFW present 23

23(22). Small black spots, with bluish-white scaling proximally, in tornus of VHW absent 24
Small black spots, with bluish-white scaling proximally, in tornus of VHW present ....***nobilis***

24(23). Blue in cell 1A+2A of DFW present as a long dash or solid block that typically forms part of a submarginal arc ....***mundula***
Blue in cell 1A+2A of DFW present as only a small basal mark or absent ..***barea***

25(22). Hindwing evenly rounded or dorso-laterally elongate 27
Hindwing a laterally elongate ellipsoid 26

26(25). Ventral surface variably pale or dark yellow, and black margin on DHW broad in apex, typically narrow in remainder ....***pedias***
Ventral surface pale yellow, and black margin on DHW narrow in apex, not present in remainder ....***pseudopedias***

27(25). Forewing length > 16mm, cell Rs of DFW with no blue or only a few blue scales at base 28
Forewing length < 13mm, cell Rs of DFW largely blue ....***azurea***

28(27). Blue on DFW extends postdiscally, ventral ground color dark yellow ......***excelsa***
Blue on DFW does not extend postdiscally, ventral ground color pale yellow ....***kingi***
29(12). One or more dark brown medial bands on ventral surface absent 37
One or more dark brown medial bands on ventral surface present 30
30(29). Submarginal ventral spots restricted to hindwing 32
Submarginal ventral spots present on both wings 31
31(30). Ventral surface with two broad medial brown bands ....***eurygonina***
Ventral surface with one faint medial brown band and a white band distally ....***sisemina tabacona***
32(30). Dark brown medial band on VFW ends at or towards apex 34
Dark brown medial band on VFW ends at mid-point of costa 33
33(32). Dark brown medial band on VFW prominent, wings pointed, disjunct subapical blue patch on DFW present ....***publius***
Dark brown medial band on VFW indistinct, wings rounded, disjunct subapical blue patch on DFW absent ....***sanjuani***
34(32). White spots in discal cell of VFW absent 36
White spots in discal cell of VFW present 35
35(34). White spot at base of discal cell of VFW absent, wings pointed ....***basilea***
White spot at base of discal cell of VFW present, wings falcate ....***bacenis***
36(34). Dark brown medial band on VFW entire ....***terambus***
Dark brown medial band on VFW restricted to an indistinct square in apex ....***syngenes***
37(29). Yellow along base of VFW absent 41
Yellow along base of VFW present 38
38(37). Yellow along base of VFW narrow, ventral purple iridescence present 39
Yellow along base of VFW very broad, ventral purple iridescence absent....***janus***
39(38). Blue on DFW a solid semicircle or triangle at base 40
Blue on DFW restricted to discal cell and anal margin ....***decorata***

40(39). Dorsal ground color dark brown, blue on DFW an apically directed triangle, pale purple at base of VFW broad and angular ....***thestias***
Dorsal ground color pale brown, blue on DFW a small semicircle, pale purple at base of VFW narrow and rather smoothly rounded ....***discus***

41(37). Dorsal surface of abdomen without prominent blue scaling 46
Dorsal surface of abdomen with prominent blue scaling 42

42(41). Black spots in tornus of VHW with prominent bluish-white scaling proximally 43
Black spots in tornus of VHW without prominent bluish-white scaling proximally ....***comosa***

43(42). Forewing pointed, hindwing vertically elongate 44
Forewing falcate, hindwing a laterally elongate ellipsoid ....***iani***

44(43). Blue on DFW a rounded semicircle 45
Blue on DFW an apically directed triangle with white scaling at apex ....***villai***

45(44). Blue on DFW occupies between basal half and third, DHW entirely blue ***virgilius***
Blue on DFW occupies between basal third and quarter, DHW predominantly blue with a block of brown scaling at middle of distal margin ....***eupolis***

46(41). Ventral surface essentially unicolorous white, gray or brown 50
Ventral surface a mixture of dark brown and pale brown pattern elements 47

47(46). Ventral surface with contrasted pale brown marks around discal cell end on both wings 48
Ventral surface without contrasted pale brown marks around discal cell end on both wings 49

48(47). Hindwing a laterally elongate ellipsoid, blue on DFW extends postdiscally ....***zostera***
Hindwing vertically elongate, blue on DFW restricted to base ....***christiani***

49(47). Both ventral wing surfaces with variably distinct darker brown costal and medial markings ....***phaeo***
Both ventral wing surfaces with a mottled mixture of pale and dark brown scales ....***busbyi***

50(46). Ventral submarginal spots absent 51
Ventral submarginal spots present 58

51(50). A semicircular area of brown scaling at costal margin of discal cell on DHW absent 54
A semicircular area of brown scaling at costal margin of discal cell on DHW present 52

52(50). Area of brown scaling in discal cell of DHW occupies upper third of cell and is not contrasted with background color, hindwing not noticeably elongate in either direction 53
Area of brown scaling in discal cell of DHW occupies upper half of cell and is a contrasted pale brown, hindwing noticeably laterally elongate ....***sobrina***

53(52). Forewing length <14mm, distal forewing margin markedly convex, ventral surface pale brown ....***apheles***
Forewing length >14mm, distal forewing margin mildly convex, ventral surface medium brown ....***thootes***

54(51). A thin dark, contrasted line at very distal margin of both ventral wing surfaces absent 56
A thin dark, contrasted line at very distal margin of both ventral wing surfaces present 55

55(54). Blue on DFW extends postdiscally ....***lycaenina***
Blue on DFW restricted to basal half ....***batesi***

56(54). Blue on DFW present 57
Blue on DFW absent ....***simplicia***

57(56). Blue on DFW semicircular, forewing rounded, ventral surface pale gray ....***hypoleuca***
Blue on DFW triangular, forewing pointed, ventral surface brown ....***nodosus***

58(50). Ventral submarginal spots present around both wings 66
Ventral submarginal spots restricted to hindwing 59

59(58). Prominent, contrasted white scaling proximal to ventral submarginal spots absent 60
Prominent, contrasted white scaling proximal to ventral submarginal spots present ....***speciosa***

60(59). Forewing costa smoothly curved, blue on DFW smoothly semicircular 63
Forewing costa mildly or strongly arched at base, blue on DFW triangular 61

61(60). Blue on DFW with an outwardly diagonal distal edge, such that blue in cell Cu2 extends significantly less far towards distal margin than that in cell 1A+2A 62
Blue on DFW with a straight or inwardly diagonal distal edge, such that blue in cell Cu2 extends as far or further towards distal margin than that in cell 1A+2A ....*cratylus*

62(61). Forewing length <16mm, distal forewing margin straight ....*theritas*
Forewing length >16mm, distal forewing margin mildly convex ....*thootes*

63(60). Ventral surface dirty white, gray or pale brown, ventral submarginal spots prominent 64
Ventral surface pure white, ventral submarginal spots weak ....*pakitza*

64(63). Blue on DFW extends little or no distance postdiscally with a curved distal margin, creating a wedge-shaped black border 65
Blue on DFW extends prominently postdiscally with a rayed distal margin, creating a black border of even width in tornal half of wing ....*lycaenina*

65(64). Blue on DFW typically restricted to lower half of discal cell and absent from cell Cu1, that on DHW typically restricted to basal two-thirds of wing, white proximal to submarginal spots on VHW absent ....*foliorum*
Blue on DFW occupies entire discal cell and base of cell Cu1, that on DHW occupies most of wing, white proximal to submarginal spots on VHW variably present ....*wallacei*

66(58). Blue either occupies both dorsal wings or if restricted to hindwing occupies entire wing 67
Blue restricted to hindwing and only occupies anal half of that wing ...*amicitiae*

67(66). Blue on DFW absent or occupies only a solid block at base 68
Blue on DFW occupies discal cell and anal margin, and has variably prominent disjunct blue rays in remainder of wing ....*atima*

68(67). Forewing length >12mm, ventral surface dirty white, gray or brown 69
Forewing length <12mm, ventral surface white ....*leucanthe*

69(68). Blue on both dorsal wings extensive, ventral surface dirty white or gray 70
Blue on both dorsal wings reduced to base, ventral surface brown ....*turneri*

70(69). Wings broad and pointed, a prominent discal cell end marking on DFW absent 71
Wings compact and rounded, a prominent discal cell end marking on DFW present ....***sticheli***

71(70). Black border on DHW narrow, ventral surface dirty white, submarginal spots on VHW more prominent in tornus ....***wallacei***
Black border on DHW broad, ventral surface pale gray-brown, submarginal spots on VHW not noticeably more prominent in tornus ....***methemona***

Biogeography

The genus *Theope* is widely distributed in the Neotropics from central Mexico, through Central America to north-west Peru, throughout the Guianas to south-east Brazil and Paraguay, and along the eastern slope of the Andes as far south as northern Argentina. The continental islands of Trinidad, and to a much lesser extent Tobago, harbor a significant *Theope* fauna that is essentially a depauperate version of what is known from the nearby mainland of northern Venezuela. A few species, all in the secondary-growth-tolerant "*virgilius*" and "*terambus* groups", have also colonised a number of smaller offshore islands, including Isla de Roatán and Isla de Bonacca [Islas de la Bahía] (Honduras), Isla de Coiba, and Isla de Puercos and Isla de Contadora [Archipiélago de las Perlas] (Panama), Curaçao and Bonaire (Netherlands Antilles), and Isla de Margarita (Venezuela). Since, with the exception of a female specimen of *T. eupolis* from Isla de Roatán, which was deemed sufficiently distinct by Godman and Salvin (1897) to be described as the distinct species *T. talna*, specimens from these islands do not significantly phenotypically differ from those on the mainland, it can be assumed that relatively regular gene flow, probably primarily through wind dispersal, is retarding phenotypic differentiation (Robbins and Small, 1981; Robbins, 1991).

Table 2. The distribution of all *Theope* species by country, with the number of recorded (solid circles) and expected (open circles) species for each country, and the percentage of the expected species recorded. Superscript numbers refer to the ranking in each row; this is not implemented in the third row for the Netherlands Antilles, which only has a single species that may not even be present as a breeding population. As in the text, species groups are arranged from the most plesiomorphic first to the most derived last.

Taxon	Mexico	Belize	Guatemala	El Salvador	Honduras	Nicaragua	Costa Rica	Panama	Venezuela	Colombia	Ecuador	Peru	Bolivia	Argentina	Brazil	Paraguay	Uruguay	Guyana	Surinam	French Guiana	Trinidad	Neth. Antilles
nobilis															●			○	○	●		
sanjuani								○		●	○											
p. publius					○	●	●	●	●	●	●	●										
p. incompositus	●	○	●	●	○																	
syngenes									○	○	●	●			●			●	○	●	○	
terambus									●	●	●	●	●	●	●	●	○	○	○	●	●	
bacenis	●	●	●	●	○	●	●	●		●												
basilea						○	●	●		●	●											
comosa										●	●	●	○		●							
zostera										○	●	●			●							
nodosus										○	●	○			○							
phaeo	●	○	●		●	●	●	●	●	●	●	●	●		●			●	○	●	●	
theritas									○	○	○	●	○		●			●	○	○		
thootes									○	○	○	●	○		●			○	○	●	○	
apheles									○	○	●	●	●		●			○	○	●	○	
sobrina									●	●	●	●	○		●			●	●	●	○	
janus									○	○	○	●			●			○	○	●		
g. guillaumei									○	○	●	○	○		●			○	○	●		
g. cecropia						○	●	○	○	○	○											
discus									○	●	●	●	○		●			○	○	●		
thestias									○	●	●	●	●	○	●	●	○	○	○	●	○	
decorata						●	●	●	○	●	●		○		●			○	○	●		
lycaenina							●	●	●	○	●	●	○		●			●	●	●	●	
leucanthe							○	○	●	●	●	●	○		●			○	○	●	●	
amicitiae															○			○	○	●		
christiani															○			●	○	○		
methemona															●							
sticheli										○	●	○	○		●							
busbyi										○	●	○			○							
turneri												○	○		●							
batesi										○	●	○			●							
atima															●					●		
foliorum							○	●	●	●	●	●	○	○	●	●		●	●	●	●	
wallacei							○	●	○	●	●	●	○		○			○	○	●		
pakitza												●	○		○							
Total recorded	12	4	9	4	8	8	20	22	16	33^5	46^1	38^3	9	2	44^2	3	0	18	7	36^4	12	1
Total expected	14	13	13	6	14	20	26	29	39^5	55^1	53^2	46^4	36	4	51^3	4	2	38	37	38	20	1
% recorded	$86^{=3}$	31	69	67	57	40	77	76	41	60	87^2	83^5	25	50	$86^{=3}$	75	0	47	19	95^1	60	100

Table 2 Cont…

Taxon	Mexico	Belize	Guatemala	El Salvador	Honduras	Nicaragua	Costa Rica	Panama	Venezuela	Colombia	Ecuador	Peru	Bolivia	Argentina	Brazil	Paraguay	Uruguay	Guyana	Surinam	French Guiana	Trinidad	Neth. Antilles
nycteis						○	●	●	●	●	●	●	○	●	●	○		●	●	●	●	
brevignoni									○	○	●	●	○		○			●	○	●		
philotes									○	●	●	●	○		●			●	●	●		
tetrastigma									○	○	●	●	○		●			○	○	●		
orphana															●			○	○	●		
hypoleuca									○	○	●	●	○		●							
simplicia															●							
azurea									●	●	●	●			●							
a. archimedes									●	○	●	●	○		●			●	○	●	○	
a. zyzyxoxyx						○	●	●	●	●	○											
m. matuta						○	●	●														
m. heureka									○	●	●											
pseudopedias	●	○	●		○	○	●	○														
pedias	●	○	●		●	○	●	●	●	●	●	●	●		●			●	●	●	●	
devriesi	●	○	●		○	○	●	●		○	●											
pepo								○		●	●											
eudocia	○	○	○		●	●	●	●	●	●	●	●	●		●			●	●	●	●	
acosma							●	●	○	●	●	●	○		●			●				
excelsa									●	●	●	●	○		●			●	○	●	●	
kingi							○	●		○	○											
barea	●	○	○		○	●	●	●	●	●	●	●	○		●			○	○	●	○	
mundula	○	○	○		●	○	○	●	○	○	●	●	○		●			○	○	●	○	
aureonitens									○	●	●	●	●		●			○	○	●	●	
galionicus									○	○	○	●			●			○	○	●		
dabrerai										○	●	○			○							
sericea									○	○	○	●	○		●			●	○	●		
lampropteryx									○	○	●	●			●			○	○	●		
eurygonina									○	●	●	●	○		●			●	○	●		
speciosa						○	●	●		●	●											
pieridoides	●	○	○	○	●	○	○	○	●	●	●		○		●			○	○	●	●	
cratylus	●	●	●	○	●	○	●	●	○	●												
s. sisemina										●	●											
s. tabacona												●										
antanitis												○	●									
iani								○		●	●											
villai	●																					
virgilius	●	●	●	●	●	●	●	●	●	●	●	●	●		●			●	○	●	●	●
eupolis	●	●	●	●	●	●	●	●														

The distribution of *Theope* diversity is dealt with here both in terms of political boundaries and the main biogeographic regions. The genus has been recorded from all Neotropical countries except Chile, where there are no appropriate habitats, and Uruguay (e.g. see Biezanko *et al.*, 1957, 1978), where it is actually possible that as many as two species might occur. From Table 2, it can be seen that Ecuador has the highest recorded number of *Theope* species, followed by Brazil, Peru, French Guiana and Colombia, but this ranking is heavily influenced by differing collecting effort in each country and does not accurately reflect biogeographic patterns. Once the expected, or "true", number of species per country has been estimated, by extrapolating the known range of each (mostly rarer) species to encompass that which it should logically occupy based on the ranges of better known species, it is evident that Colombia should harbor the highest number of species, followed by Ecuador, Brazil, Peru and Venezuela. This biogeographic pattern of species distribution for the large genus *Theope* also accurately reflects the distribution of overall diversity in the family Riodinidae, although there are not enough data at present to determine whether Peru or Brazil occupies the third position (Hall, unpubl. data). It is difficult to estimate the "true" diversity of the genus *Theope* in certain countries on the periphery of common species' ranges, and thus the predicted number of species for countries such as Nicaragua, Venezuela, Bolivia and Trinidad, where, at least in the first three cases, there has also been relatively little riodinid collecting, may be slightly underestimated.

It is interesting to note that the order of this list is quite accurate even in spite of the fact that *Theope* is almost exclusively a lowland-inhabiting genus, and in fact, when montane faunas are taken into consideration, overall riodinid diversity in the Andean countries is seen to be even higher with respect to the Guianas and Brazil, the relatively small endemic fauna in the Atlantic coastal forests and large size of the latter country not being sufficiently compensatory (Hall, unpubl. data). For example, the ratio of overall riodinid diversity between the lepidopterologically relatively well studied countries (see column three of Table 2) of French Guiana (Brévignon and Gallard, 1997a,b, 1998a,b,c) and Ecuador (Hall and Willmott, unpubl. data) is at least 1:2, whereas the data in column two of Table 2 indicate that for *Theope* alone, this ratio will be only about 1:1.5. The reason for the megadiversity of riodinids (and Lepidoptera in general) in Colombia and Ecuador is clear: these countries not only encompass large Amazonian and cloud forest Andean faunas, but also a diverse and highly endemic Chocó fauna to the west of the Andes (Callaghan, 1985, 1993; Hall and Willmott, unpubl. data), and more intensive sampling in the latter two regions has only recently begun to more fully elaborate their true diversity (Salazar and Constantino, 1993; Willmott and Hall, 1994; Hall and Willmott, 1995a,b,c, 1996a,b,c, 1998a,b,c; Callaghan and Salazar, 1997; Hall, 1998b). The common misconception in the literature (e.g. Brown, 1991, 1996a) that Brazil and Peru harbor the highest number of riodinid and other butterfly species in the Neotropics (and thus the world) is largely due to disproportionately high sampling in those countries and a lack of published information on the lepidopteran diversity of Colombia (but see Constantino, 1998) and Ecuador.

To briefly turn to conservation, I perform a "critical faunas analysis" for *Theope*, as first implemented by Ackery and Vane-Wright (1984) for danaine butterflies and subsequently used by a number of authors, including Collins and Morris (1985) for papilionid butterflies and Pearson and Cassola (1992) for cicindelid beetles. Countries are ranked primarily in order of the number of endemic *Theope* species they possess and secondarily, if this number is equal in two or more countries, in order of the number of previously unrepresented species on the list they possess, with the objective of highlighting a minimum number of countries required to include all species, which can then be targeted for conservation effort. Using the recorded number of *Theope* species from each country

(Table 3), nine such countries are highlighted, but using the expected number from each country (Table 4), and thus once the spurious endemics have been removed, this number is reduced to four. I am not aware that any such comparison has ever previously been made, but it is instructive, and the perils of inadequate information for conservation planning are obvious.

It is important to note that the ranking list in Table 4 for *Theope* exactly matches that in Collins and Morris (1985) for Neotropical Papilionidae, if the spurious French Guianan endemic *Parides vercingetorix* (Oberthür, 1888) is removed (it is expected to occur in neighbouring Amapá state, Brazil (Tyler *et al.* (1994)) and their countries in my ranks three and four are similarly regarded as inseparable pairs. It also closely matches that in Pearson and Cassola (1992) for Neotropical cicindelid beetles. The fact that critical faunas analyses also generated very similar rankings for danaines and papilionids in the Oriental region (Vane-Wright *et al.*, 1991), provides further evidence to suggest that such analyses can be collated for a diverse range of organisms to pin-point biological "hot-spots" of high endemism and diversity for the highest conservation priority. Despite the pessimism of Brown (1993), these comparisons also serve to illustrate that, once systematic problems have been eradicated, lycaenoid butterflies can successfully be used as accurate bioindicators and may in the future prove to be among the best. In an effort to reduce the overemphasis on endemics and introduce other measures of diversity, Vane-Wright *et al.* (1991) introduced the concept of taxic weighting to give a measure of taxonomic distinctness, as gleaned from cladistic classifications, to be used either in isolation or in conjunction with critical faunas analysis. Although a thought-provoking first step in the direction of using other diversity measures for conservation prioritising, in its current format this particular proposal suffers from a slight overweighting of basal taxa, although

Tables 3 (above) and 4 (below). Analyses of critical *Theope* faunas of the Neotropics based on recorded (above) and expected (below) numbers of species per country. Countries are listed in order of conservation importance on the basis of the following criteria (after Ackery and Vane-Wright, 1984): A = number of endemic species; B = number of non-endemic species not occurring in previously listed countries; C = total number of newly added species; D = cumulative number of species. In Table 4, ranks three and four could equally well be taken by the two countries listed in each case; I currently regard as probable true Brazilian endemics, *T. simplicia* and *T. methemona*, and as a true Mexican endemic, *T. villai*. The site conservation efficiency (Pressey and Nicholls, 1989) for minimal representation of *Theope* is 0.82 in Table 4.

Country	A	B	C	D
1. Ecuador	3	43	46	46
2. Brazil	3	8	11	57
3. Panama	1	3	4	61
4. Mexico	1	1	2	63
5. Peru	1	0	1	64
6. French Guiana	1	0	1	65
7. Colombia	1	0	1	66
8. Guyana	1	0	1	67
9. Bolivia	1	0	1	68

Country	A	B	C	D
1. Brazil	2	49	51	51
2. Mexico	1	6	7	58
3. Col/Ecdr	0	9	9	67
4. Peru/Bolivia	0	1	1	68

Table 5. The distribution of all *Theope* species by major biogeographical region, with the number of recorded (solid circles) and expected (open circles) species and endemics for each region. I use the following definitions for the nine biogeographical regions: Mexico - political boundaries of Mexico; C. America - region (all countries) between and including Guatemala and east-central Panama; Chocó - east Panama to west Ecuador; Andes - exclusively above 1500m along length of Andes; U. Amazon - a broad semicircle in western Amazon, with Manaus (Brazil) as eastern-most point; L. Amazon - all Amazon east of Manaus and aforementioned semicircle; Guianas - political boundaries of Guyana, Surinam and French Guiana; Trinidad - Caribbean islands of Trinidad and Tobago; S. E. Brazil - entire area to east and south of Amazon basin covering south-east South America. As in the text, species groups are arranged from the most plesiomorphic first to the most derived last.

	W. of Andes				E. of Andes				
Taxon	Mexico	C. America	U. Amazon	Andes	U. Amazon	L. Amazon	Guianas	Trinidad	S. E. Brazil
nycteis		●	●		●	●	●	●	●
brevignoni					●	○	●		
philotes					●	●	●		
tetrastigma					●	●	●		
orphana						●	●		●
hypoleuca					●	●			
simplicia					○	●			
azurea					●				
archimedes		●	●		●	●	●	○	
matuta		●	●						
pseudopedias	●	●							
pedias	●	●	●		●	●	●	●	●
devriesi	●	●	●						
pepo			●						
eudocia	○	●	●		●	●	●	●	●
acosma		●	○		●		●		
excelsa					●	●	●	●	
kingi		●	○						
barea	●	●	●		●	○	●	○	
mundula	○	●	○		●	●	●	○	●
aureonitens					●	○	●	●	
galionicus					●	○	●		
dabrerai					●				
sericea					●	●	●		
lampropteryx					●	●	●		
eurygonina					●	●	●		
speciosa		●	●						
pieridoides	●	●	●			●	●	●	●
cratylus	●	●	●						
sisemina				●					
antanitis				●					
iani			●						
villai	●								
virgilius	●	●	●		●	●	●	●	●
eupolis	●	●							

	W. of Andes				E. of Andes				
Taxon	Mexico	C. America	Chocó	Andes	U. Amazon	L. Amazon	Guianas	Trinidad	S. E. Brazil
nobilis						●	●		
sanjuani			●						
publius	●	●	●						
syngenes					●	●	●	○	
terambus					●	●	●	●	●
bacenis	●	●	○						
basilea		●	●						
comosa					●				
zostera					●				
nodosus					●				
phaeo	●	●	●		●	●	●	●	●
theritas					●	●	●		
thootes					●	●	●	○	
apheles					●	○	●	○	
sobrina					●	●	●	○	●
janus					●	●	●		
guillaumei		●	○		●	○	●		
discus					●	●	●		
thestias					●	●	●	○	●
decorata		●	●		●	●	●		
lycaenina		●	○		●	●	●	●	●
leucanthe		●	●		●	●	●	●	●
amicitiae						○	●		
christiani						○	●		
methemona						●			
sticheli					●	●			
busbyi					●				
turneri					●	○			
batesi					●	●			
atima					●	●			
foliorum		●	○		●	●	●	●	●
wallacei		●	●		●	○	●		
pakitza					●				
TOTAL	12/14	26	20/27	2	45/46	34/45	38	12/19	14
ENDEMICS	1	1/0	3	2	8/7	2/1	2/0	0	0

this is easily rectified, but mainly from the necessity to have a detailed hypothesis of phylogenetic relationships at hand, something which is, of course, available only for an infinitessimally small proportion of the world's biota.

When considering broader patterns of geographical distribution in *Theope*, as illustrated in Table 5, it can immediately be seen that the genus is predominantly Amazonian (75%), with only 46% of species occurring in the Transandean region, and that most species are restricted to one side of the Andes, with only seventeen species (25%) occurring widely on both slopes. The highest number of recorded species for any region occurs in the upper Amazon basin, although the biologically more meaningful expected numbers are only marginally higher than those for the lower Amazon; however, even the expected number of endemics in the upper Amazon is considerably higher than anywhere else. If *Theope* is at all representative of essentially entirely lowland genera, these data suggest that the often reported high species diversity of riodinids in the upper Amazon (Brown, 1984; Emmel and Austin, 1990; Lamas *et al.*, 1991; Lamas, 1994; Robbins *et al.*, 1996) is not due to the inherently greater diversity of the region, when compared to the lower Amazon, but almost entirely to the inclusion of additional species that are restricted to a narrow band at the base of the eastern Andes. Since *Theope* species are largely lowland wet forest habitat generalists, single site diversity should closely match that for its entire surrounding region, as it does in perhaps the most thoroughly collected Amazonian country, French Guiana, where thirty-six species can be encountered in the environs of Cayenne (Brévignon and Gallard, pers. comm.), matching the recorded total for the entire country (see Table 2). Collecting has not been as intensive in the western Amazon until recently, and there the closest example of single site diversity matching the regional diversity is that of thirty-three species known from the vicinity of Tena, at the base of the eastern Andes in Ecuador (Hall and Willmott, unpubl. data). The low numbers of *Theope* species in the latest published lists for sites in Rondônia, Brazil, and Madre de Dios, Peru (Lamas, 1994; Robbins *et al.*, 1996; Hall and Austin, 1997), indicate that this genus and, by extrapolation, the riodinids as a whole are still well underestimated there. Based on the distributional data presented in this work for *Theope* and my knowledge of the distributional data of other genera in the family, it is evident that riodinid species diversity will be approximately the same in any site that encompasses a wide range of microhabitats, in the upper river drainages of the "megadiversity" countries (*sensu* Mittermeier, 1988) of Colombia, Ecuador, Peru and perhaps to a slightly lesser extent Brazil (Robbins *et al.*, 1996; Robbins & Opler, 1997). This distribution of Amazonian diversity in riodinid butterflies closely matches that of other organisms such as birds, mammals, amphibians and angiosperms (Myers, 1988; McNeely *et al.*, 1990; Robbins & Opler, 1997).

Another point of biogeographical interest in Table 5, is that certain well-known centers of faunal endemism, such as the Guianan shield and the Atlantic coastal forests of south-east Brazil, harbor no expected *Theope* endemics, but the Chocó does contain a relatively high percentage of endemics, similar to that found in other riodinid genera (Callaghan, 1985; pers. obs.). As discussed below, only the two members of the "*sisemina* group" are believed to be exclusively restricted to cloud forest Andean habitats. Other notable patterns at the species-group level, include the complete restriction of the "*tetrastigma*" and "*hypoleuca* groups" and predominant restriction of the "*nycteis*", "*sericea*", "*theritas*" and "*foliorum* groups" to the Amazon, and the predominant restriction of the "*pedias*" and "*virgilius* groups" to the Transandean region. The "*terambus* group" presents a curious biogeographic pattern by having three probable sister species pairs each inhabiting either one side of the Andes or the other, suggesting that each pair speciated within its current biogeographic region, presumably speciating in allopatry within reduced forest refugia and then expanding their ranges to overlap each other. Finally, it is noticeable from Table 5 that almost all species in the most derived species groups are restricted to the Amazon basin and this suggests, given the high species diversity in these groups, that the most recent diversification in *Theope* has occurred in this region.

Biology

Habitats and Ecology of Adults

Habitats

Theope species predominantly occur only in wet forest habitats, and they are very rarely ever encountered in drier regions (e.g. Ebert, 1969; de la Maza and Bezaury, 1992; de la Maza and Gutiérrez, [1994]), although certain species in the "*virgilius*" and "*terambus* groups" are tolerant of seasonally dry cerrado, semi-deciduous and mixed *Acacia* forests and *T. pieridoides* appears to almost exclusively occur in moist and semi-deciduous habitats (see Fig. 8). The ventral ground color in populations of "*virgilius*" and "*terambus* group" species that live in dry habitats tends to be paler than that in populations which inhabit wet forests, and, by extrapolation, it seems plausible that the unique white coloration of *T. pieridoides* in the genus represents a species-wide adaptation to the paler pastel colors of drier habitats. Most *Theope* species also occur exclusively in primary forest habitats, but there are exceptions. *T. eudocia* exemplifies a species that occurs only in secondary growth areas, and certain members of the "*pedias*", "*foliorum*" and "*thestias* groups" appear to be most consistently encountered in marginal forest habitats. In the latter group, the reality of such a habitat distribution is supported by the fact that the hostplant of its only reared species, *T. guillaumei*, is *Cecropia*, a widespread genus of secondary growth trees (see Table 7).

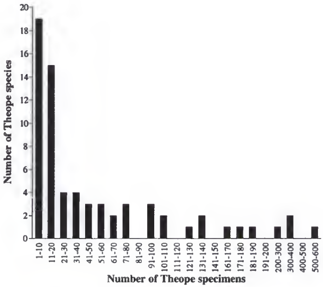
Like most nymphidiine genera, *Theope* is almost exclusively a lowland forest genus and while a few species, such as *T. virgilius* and *T. phaeo* are regularly encountered above 1000m, only one species, *T. sisemina*, is known to be a cloud forest specialist, occurring between 1500 and 2000m, although its sister species, *T. antanitis*, will probably be shown to have a similar altitudinal range when detailed locality data become available. The overwhelming predominance of lowland species in myrmecophilous genera is presumed to be related to the decline in ant species diversity with increasing altitude (Olson, 1994; DeVries, 1997).

Rarity

Theope species are poorly represented in all but the largest museum collections and only two, the BMNH and USNM, contain more than two-thirds of the known species. It is rather a sad indictment on the state of the world's riodinid collections in general, in comparison to those of other butterfly groups, that K. R. Willmott and I have managed to amass the fifth largest collection of *Theope* during only a few years of collecting and from only a single country (see list of collections in "Methods" section and Table 2 for details). The reasons for this paucity of material and why entomologists have tended to overlook them are twofold. Firstly, *Theope* species are small and inconspicuous, sometimes rather drab, and have in the past been difficult to identify, but secondly, and more importantly, the majority of them are genuinely rare.

On a scale of one to five of decreasing rarity, Brown (1993), in a generic overview of lycaenoid butterflies, gave *Theope* a "two", a number I believe to accurately assess its average rarity in the context of the Riodinidae. However, a good number of *Theope* species are substantially rarer than this and from Figure 5, it can be seen that half of all species are

Fig. 5. A graph illustrating the number of *Theope* specimens examined per described *Theope* species in bands of ten specimens up to two hundred, and thence in bands of one hundred specimens up to six hundred.



known from twenty or fewer specimens, while nineteen species (28%) are known from ten or fewer specimens. Although, of course, I have not examined every extant *Theope* specimen, my coverage of collections and correspondence with lepidopterists has been extensive and I believe these numbers for rarer species to be reasonably accurate. It is almost certain that five *Theope* species, *T. antanitis*, *T. busbyi*, *T. christiani*, *T. pakitza* and *T. turneri* are known only from their unique types and that a further five species, *T. antanitis*, *T. atima*, *T. christiani*, *T. methemona* and *T. sanjuani* have not been collected in at least the last fifty years. Under the categories established by the International Union for Conservation of Nature and Natural Resources (IUCN) (e.g. Collins and Morris, 1985), these latter species would actually be deemed extinct, an absurd deduction, given the extensive remaining habitat (Tyler *et al.*, 1994) and the fact that these species have not been specifically sought. Since there are no *Theope* species endemic to the most severely threatened Neotropical habitats, such as south-east Brazilian Atlantic forest (Brown, 1991, 1996a,b; Brown and Brown, 1992) and west Ecuadorian moist and dry forest (Myers, 1988; Dodson and Gentry, 1991; Parker and Carr, 1992), none is imminently threatened with extinction. The only *Theope* species that might currently be deemed vulnerable in conservation terms are the very rare *T. villai* and *T. antanitis*, which are both known only from highly restricted ranges in western Mexico and the Bolivian Andes, respectively, where they are also under threat from habitat destruction.

It is clear that the IUCN categories are far from adequate for assessing rarity in species-rich tropical communities (Mace and Lande, 1991; New, 1996) and a number of other rarity indices have been proposed, including the "coefficient of abundance" of Corbet (1946) and the "DACOR rating" of Parsons (1992, 1998), but even these barely begin to describe the numerous facets of rarity. A number of more complex models have been devised (e.g. Ferrar, 1989), and all recognise three main factors that contribute to the rarity of a species, namely its degree of habitat (macro and micro) specificity, the extent of its geographical range and its local population size. Combinations of these factors produce at least seven categories to describe the true rarity of a species in nature, but even then there are several confounding reasons why its perceived rarity may differ, including variations in seasonal abundance and abundance over the range of the species, and the competence and expertise of the surveyor. With very few exceptions, *Theope* species do not tend to be habitat specialists in the strictest sense; most occur in all wet forest habitats, most are not restricted to small ranges and there is no evidence, at least in equatorial regions, that their population numbers are strongly influenced by the seasons. Field experience indicates that the true rarity of *Theope* species can simply be explained by very low population densities, but the main reason they are so poorly represented in collections is that many are very local. This fact is well exemplified by the "*sericea* group", most of whose species are very rare in collections (and typically not represented at all) but actually locally common on hilltops, where perching males aggregate (see below).

Ecology

Theope males are most frequently encountered perching on hilltops and ridgetops, in much the same manner that birds and other vertebrates and insects have been described to lek (see Höglund and Alatalo, 1995). In fact, the species of some groups, such as the "*theritas*" and "*sericea* groups", are virtually never found anywhere else; only in the "*pedias*" and "*thestias* groups", whose species typically frequent secondary growth and streamside habitats, is this behavior rarely seen. Scott (1975) defined perching behavior as "males resting at characteristic sites and investigating objects by flying out at them in search of females", a definition that fits well within the concept of lekking, as first coined by Lloyd (1867), despite the fact that this latter term has infrequently been used with respect to butterflies; the word "lek" comes from the Swedish verb "leka", meaning "to play", and in early Scandinavian meant "performing with rapid movements" (Höglund and Alatalo, 1995). The weight of evidence from the Lepidoptera literature supports the prevailing hypothesis that hilltops, as prominent topographical features, act as rendezvous sites for the sexes and that hilltopping behavior is a mechanism to enhance mating success in rarer species, whose foodplants similarly exist at a low density (Shields, 1968; Scott, 1968, 1975, 1983). A common objection to this theory is that females are rarely found on hilltops, but mating is presumably often rapid and inconspicuous (Miller and Clench, 1968), and Shields (1968) demonstrated experimentally, using a Nearctic papilionid, that only virgin females returned to the hilltop, when released away from it. It is well established that many riodinid genera exhibit interspecific differences in male perching behaviors in terms of perching time, height and microhabitat type (Callaghan, 1983;

Brévignon and Gallard, 1995; Hall, 1998b, pers. obs.), and these have been explained in terms of premating isolating mechanisms (Callaghan, 1983), as first codified by Dobzhansky (1937) and Mayr (1963). All three of the aforementioned isolating mechanisms are seen in *Theope*, but since the majority of species for which perching data are available are hilltoppers, the following discussion will center on those mechanisms that allow isolation within the close confines of a hilltop.

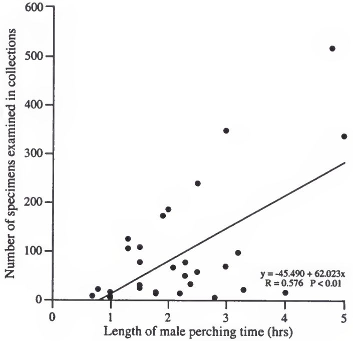
A consideration of the length of male perching times of thirty-one *Theope* species (see Table 6), including representatives from all species groups except the "*thestias* group", indicates that the average length of time a species spends perching is 2.3 hours, somewhat longer than the 1.8 hours calculated by Callaghan (1983) in his study of four *Theope* species. This is a shorter period of time than has been reported for Nearctic lycaenoid butterflies (Scott, 1975), but is about average for the Riodinidae, being longer than that for *Argyrogrammana*, *Alesa* Doubleday, 1847, and *Anteros* Hübner, [1819], but shorter than that for *Ancyluris* Hübner, [1819], and *Nymphidium* (Callaghan, 1983; Brévignon and Gallard, 1995; pers. obs.). It is interesting to note that when these same *Theope* species are divided into hilltoppers (n=25) and non-hilltoppers (n=6; marked in Table 6 by an "*"), the figure for the former is 2.0 hours and that for the latter is 3.2 hours. Although the sample size for non-hilltoppers is small, with the caveat that phylogenetic problems undoubtedly affect the independence of data points, the difference between the two groups is significant (t-test: P=0.02), suggesting that, in *Theope*, hilltoppers do spend less time perching than non-hilltoppers. However, considerably more data from other riodinid genera are needed before this hypothesis can be confidently accepted or rejected as a general phenomenon. If true, this finding might be explained by an increased threat of predation on a predictably concentrated aggregation of hilltopping individuals, often of many species. There is notable

Table 6. A pictorial list of recorded male perching times for thirty-five species of *Theope*, including representatives from each species-group, with mean perching times for each species and species-group and the length of time spent perching for each species and means for each species-group. All species perch on hilltops, except those marked with an "*". All perching times are based on data collected by myself and K. Willmott in Ecuador, except the following: *T. orphana* - data given on specimens in USNM; *T. archimedes* and *T. matuta* (lower limit of 12:00 hrs only) - DeVries (1997); *T. acosma* (08:30-09:20 hrs only), *T. virgilius* (11:40-15:00 hrs only), *T. terambus* and *T. theritas* (identification uncertain, see text) - Callaghan (1983).

Taxon	Time of Day (hrs)																																					Mean Perching Time for Species	Mean Perching Time for Group	Number of Hours		Species Included per Group
	0815-0830	0830-0845	0845-0900	0900-0915	0915-0930	0930-0945	0945-1000	1000-1015	1015-1030	1030-1045	1045-1100	1100-1115	1115-1130	1130-1145	1145-1200	1200-1215	1215-1230	1230-1245	1245-1300	1300-1315	1315-1330	1330-1345	1345-1400	1400-1415	1415-1430	1430-1445	1445-1500	1500-1515	1515-1530	1530-1545	1545-1600	1600-1615	1615-1630	1630-1645	1645-1700	1700-1715	1715-1730			Length of Perching Time for Species	Length of Perching Time for Group	
nycteis		●	●	●	●	●	●															●	●	●	●	●	●	●	●	●								1157		3.8		
brevignoni																						●	●	●	●													1400		1		
philotes			●	●	●	●	●															●	●	●	●	●	●	●	●	●								1157	1238	3.2	2.7	3/3
tetrastigma																									●	●	●	●	●	●	●	●	●					1525		2.2		
orphana																																●	●	●				1625	1555	0.7	1.5	2/2
*azurea**																				●	●	●	●	●	●	●	●	●	●									1415	1415	2.5	2.5	1/3
archimedes																●																						1200		-		
matuta																●	●	●	●	●	●	●	●	●	●	●	●											1330	1245	3	3	2/2
*pedias**																●	●	●	●	●	●	●	●	●	●	●	●											1330		3		
*pepo**																●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●							1400	1345	4	3.5	2/4
*eudocia**								●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●											1230		5		
acosma		●	●	●	●																			●	●	●	●	●	●	●								1157	1213	2.4	3.7	2/2
excelsa																				●	●	●	●	●	●	●	●	●										1408		2.3		
barea																				●	●	●	●	●	●													1345		1.5		
mundula																				●	●	●	●	●	●	●	●	●										1413		2.1		
aureonitens																						●	●	●	●	●	●											1415		1.5		
dabrerai																								●	●	●	●											1430		1		
lampropteryx																						●	●	●	●	●	●											1415	1410	1.5	1.6	6/9
eurygonina																				●	●	●	●	●	●	●	●	●										1409	1409	2.3	2.3	1/4
sisemina																				●	●	●	●															1310	1310	1	1	1/2
iani																			●	●	●	●	●	●	●													1338		1.8		
virgilius															●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●					1405	1351	4.8	3.3	2/4
*publius**																				●	●	●	●	●	●	●	●											1400		2		
terambus																		●	●	●	●	●	●	●	●	●												1343		1.9		
basilea																															●	●	●	●	●	●		1638	1446	1.3	1.7	3/7
comosa																		●	●	●	●	●	●	●														1323		1.8		
zostera																		●																				1200		-		
nodosus													●	●	●	●	●	●	●	●	●	●	●															1238		2.8		
phaeo																					●	●	●	●	●													1353		1.3		
theritas																					●	●	●															1338		0.8		
apheles												●	●	●	●	●	●	●	●	●	●	●	●	●														1238		3.3		
sobrina																●	●	●	●	●	●																	1245	1259	1.5	1.9	7/8
*thestias**																				●																		1300		-		
*decorata**																						●																1330	1315	-	-	2/5
*lycaenina**																		●	●	●	●	●	●	●	●	●	●											1345	1345	2.5	2.5	1/13
TOTAL	0	2	3	3	3	2	2	1	1	1	1	2	3	3	4	9	8	12	12	20	21	26	25	24	23	19	18	10	7	5	4	4	4	2	1	1	0	1338		2.3		35/68

variation in the length of perching time even between the hilltopping species groups, but given the incompleteness of data for most groups, it is just worth pointing out that, on average, members of the "*sericea* group" spend a well below average time perching (1.6 hours). Interestingly, a plot of the length of time spent perching against the number of specimens examined in collections (those listed in the "Methods" section) (Fig. 6a) for each of the same thirty-one species gives a significant positive correlation (P<0.01), indicating that, at least in part, certain species are rare in collections because they perch only for a short period of time and, as outlined above, probably because they are hilltoppers.

Fig. 6a. A graph illustrating the significant positive correlation for thirty-one *Theope* species between the number of hours a male spends perching and the number of specimens that have been examined in collections (listed in the "Methods" section) for that species.



When considering the specific period of time over which each of thirty-five *Theope* species perches, a clear pattern emerges (Table 6, Fig. 6b) in which only a handful of species perch in mid morning (beginning at 0830h), followed by a trough in late morning and then a sharp peak in numbers around the boundary of early and mid afternoon (between 1300 and 1500h) that tapers off markedly to end in the middle of the late afternoon (1715h). The mean perching time for this set of *Theope* species is 1338h, and during the modal period of 1330-1345h, twenty-six species (74%) are perching. All perching riodinid genera have characteristic perching time profiles, as seen in Figure 6b, and that of *Theope* represents a common pattern for the family; its mean perching time also roughly corresponds with the peak perching activity time for the family (Hall and Willmott, unpubl. data). Again, although the data are incomplete, certain patterns are notable at the species group level. For example, members of the "*nycteis* group" tend to perch in the early morning and then again in the afternoon, those of the "*tetrastigma* group" perch in the later part of the afternoon, and those of the "*theritas* group" have a mean perching time that is significantly earlier than that in other large hilltopping groups such as the "*sericea* group".

Fig. 6b. A graphic representation of the total perching figures given in Table 6 for thirty-five *Theope* species, illustrating the number of species perching in each fifteen minute interval, throughout the daylight hours in which riodinids are active.

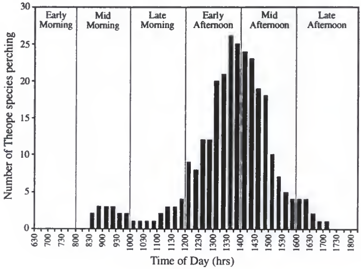
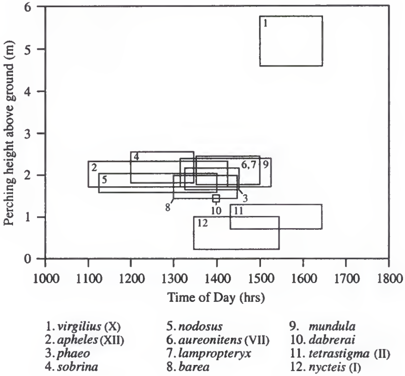


Fig. 6c. A graphic representation of the extent to which two male perching parameters, time of day and height above ground, contribute to niche partitioning and reproductive isolation in twelve *Theope* species that are regularly encountered on a single hilltop at Finca San Carlo, near Tena, in eastern Ecuador. The list of species is organised into groups and the species-group number is given in parentheses at the first mention of a component species.



In exceptional circumstances, as many as fifteen *Theope* species may be found perching on a single hilltop. Figure 6c illustrates the degree to which the variables of time of day and height above the ground aid in creating a specific perching niche for each of the twelve species (representing five species-groups) that are regularly encountered on a hilltop at Finca San Carlo, near Tena, in eastern Ecuador (as described and illustrated in Hall and Willmott (1995a)). Here, *T. nycteis*, like all members of the "*nycteis* group", occupies a distinct perching niche within a meter of the ground, as does *T. tetrastigma* slightly higher and *T. virgilius* much higher, in the lower branches of a small tree in this case, but the remaining eight species, of the "*sericea*" and "*theritas* groups", all cluster together about two meters above the ground, and are only minorly separated by their perching times. This is in contrast to the results of Callaghan (1983 - 10 genera [2-6 species in each]) and Brévignon and Gallard (1995 - *Argyrogrammana* [13 species]), whose studies of several riodinid genera suggested, with very few exceptions, that each species occupied a locally unique perching window in time and space, even despite the fact that Callaghan (1983) did not use height above the ground as an additional perching parameter. Since the assumption of the existence of unique perching niches in time and space has been used, without even using morphology as corroborating evidence, to both question the distinctness of species (Brévignon and Gallard, 1995, 1998a) and genera (Callaghan, 1983) when it appeared to break-down, and to justify the description of new species (Brévignon and Gallard, 1998a) when little else but differing perching niches of this kind were apparent (in different geographic locations), I believe the validity and universal applicability of the assumption need to be carefully scrutinised.

When an apparent break-down of this assumption does occur, Callaghan (1983) invokes phenotypic dissimilarity as a mitigating reason, suggesting that, at a given time and place, females will not have trouble distinguishing between quite different-looking males anyway, and vice versa. However, the evidence in Table 6 and Figure 6c indicates that phylogeny is an important factor influencing the perching behavior of a particular species and that in fact, members of a monophyletic species group are more likely to perch at the same height and time and, to a lesser extent, for the same period of time as each other, as they are with any other species. Therefore, it is actually much more likely that similar-looking species will share very similar perching niches, and since we know that reproductive isolation is maintained among these species, we must look to a different answer than phenotypic dissimilarity to explain why this is so. All of the eight species in Figure 6c whose perching niche is so similar may be encountered on that hilltop over a period of two or three days and the majority in a single day, and, although there is some horizontal spacing within an area of about $6m^2$, no one species consistently occupies a particular clump of leaves. Therefore, seasonality and horizontal spacing can not, in this case, be invoked as "hidden" reasons for the apparent overlap in perching niches. Furthermore, field experience indicates that such a scenario is in no way confined to *Theope* but is actually a widespread phenomenon that has already been reported for *Sarota* (Hall, 1998b).

Based on all the information presented above and a process of elimination, I suggest that the problem of apparent partial or entire overlap in the perching niches of many species can be explained by the previously unrecognised, or at least seriously underestimated (see Callaghan, 1983), widespread use of species-specific pheromones disseminated predominantly by as yet largely unknown soft glandular tissues or organs that are not apparent after traditional dissection techniques, employing immersion of thoraces or abdomens in potassium hydroxide (KOH). This assertion is perhaps supported by an observation by DeVries (1997) that a bright yellow gland was extruded laterally from the second thoracic segment in the riodinid *Chorinea octavius* (Fabricius, 1787). Our understanding of such disseminating glands is likely to be best enhanced by careful field observations of live individuals and, by virtue of their species-specific function, their shape, color and position, if present, are likely to prove of great taxonomic value. In conclusion, it is worth emphasising that the largest data set ever presented on male perching behavior for a single riodinid genus indicates that overlap of perching niches for closely related riodinid congeners, in the obvious and highly visual categories of time and space, is not an exception to the rule, but, rather, a common phenomenon. Thus, whether certain individuals do or do not exhibit such perching niche overlaps should not be used in whole or substantial part to justify or influence decisions concerning their taxonomic status.

The males of most *Theope* species are encountered perching as solitary individuals, infrequently in groups of two or three, and only very rarely in larger numbers (e.g. *T. pepo* and *T. lycaenina*), thus explaining why they are very rarely seen engaged in aerial spiralling with other, usually conspecific, males, as is common in many other riodinid genera. Their flight is typically fast and erratic. All species in the genus (at least those observed) are unusual in the family Riodinidae for resting beneath leaves, or very occasionally on top of leaves, with their wings closed over their bodies instead of spread open. This resting posture is known to occur in the Nymphidiini only in "*Pandemos*" *godmanii* Dewitz, 1877 (DeVries, 1997), the sister species to *Theope* (Hall, in prep.), and the unrelated genus *Setabis* (pers. obs.), indicating that this behavior has evolved twice in the tribe (Hall, in prep.). The much scarcer females are most frequently encountered in forest lightgaps or along forest edges and I have only rarely seen them in the vicinity of male perching areas. I have only observed two species *in copulo*, both in such male perching areas, *T. pepo* at 1400h, in the middle of that male's perching period, and *T. sobrina* at 1200h, at the beginning of that male's perching period. The copulatory position in both cases while at rest was back-to-back with wings closed.

Seventeen *Theope* species, of both sexes, have been recorded nectaring at a variety of flowers and those that have been identified include *Cordia* (Boraginaceae), *Terminalia* (Combretaceae), *Croton* (Euphorbiaceae), *Tetrathylacium* and *Casearia* (Flacourtiaceae), *Pentaclethra* and *Inga* (Leguminosae = Caesalpinioideae, Faboideae, Mimosoideae and Papilionoideae Auctt.), *Psychotria* (Rubiaceae), *Serjania* (Sapindaceae) and *Lantana* (Verbenaceae) (Ross, 1976; DeVries, 1997; pers. obs.). Flower visitation in *Theope* is uncommonly seen and records are known only for eight species groups, most of which, including the "*archimedes*", "*pedias*", "*eudocia*", "*virgilius*", "*terambus*", "*thestias*" and "*foliorum* groups", contain a large proportion of forest edge inhabiting species.

Interestingly, only two true forest-dwelling species, in the "*theritas* group", have been observed to visit flowers, on medium-sized bushes in forest lightgaps (pers. obs.), suggesting that probably most forest-dwelling *Theope* species also visit flowers, but out of sight in the subcanopy and canopy.

No *Theope* species has been recorded puddling and only three species, *T. acosma*, *T. virgilius* and *T. discus*, including both the sexes, have been recorded as attracted to rotting carrion (see Hall and Willmott, in press). While the latter behavior is common in certain riodinid subfamilies/tribes, including the Euselasiinae Kirby, 1871, Riodinini Grote, 1895 (*sensu* Harvey, 1987), and Helicopini Reuter, 1897 (*sensu* Hall, 1998b), it is only very rarely known to occur in any myrmecophilous tribes, suggesting perhaps that essential nutrients have already been acquired by the larvae from, for example, feeding at extrafloral nectaries or on membracids (Hall and Willmott, in press); such nutrients would then not need to be acquired by the adults, most notably the males, which are now widely believed, based on studies of non-riodinid butterflies, to supply females with a significant proportion of their nutrients through spermatophore transfer (Boggs and Gilbert, 1979; Sculley and Boggs, 1996).

The sex ratio of all sexually reproducing organisms is theoretically expected to be 1:1 (Fisher, 1930), although the females of most butterfly species, including those of *Theope*, are more poorly represented in collections than males because they are less readily observed and collected. It is thus extraordinary to find in two "*thestias* group" species of *Theope*, namely *T. decorata* and *T. guillaumei*, a strongly female-biased sex ratio of about 6:1. This phenomenon appears to be genuine, given its occurrence in wild-caught and reared groups of individuals (see the individual species accounts), but more rearing data from this species group are certainly needed. Such strongly female-biased sex ratios of reared butterflies have previously been reported only in the nymphalid genera *Hypolimnas*

Hübner, [1819], *Acraea* Fabricius, 1807, and *Danaus* Kluk (Poulton, 1924; Owen, 1971; Clarke *et al.*, 1975; Smith, 1975; Clarke, 1984; Smith *et al.*, 1998), the prevailing explanations being either meiotic drive of the Y chromosome (Owen, 1971), very high mortality of males in the pre-adult stage due to an infective cytoplasmic factor (Clarke *et al.*, 1975), or nuclear-cytoplasmic incompatability (Smith *et al.*, 1998).

Available evidence from label data and my own field experience suggests that in wet tropical habitats, *Theope* species do not undergo substantial seasonal population fluctuations, and it is notable that, as a general rule, riodinid species diversity and individual abundance do not drop markedly in the dry season as they do in certain other butterfly groups, especially the Nymphalidae (Hall and Willmott, unpubl. data). However, it is likely that in the dry regions of Mexico, Central America and southern South America, the genus is rarer or absent in the middle of a harsher dry season.

Morphology and Ecology of Immature Stages

Hostplants

Although the first description of *Theope* immature stages was given by Guppy (1904) at the beginning of the twentieth century (see Fig. 9), it is only in recent years that more concerted and intensive searching for riodinid early stages has led to further such discoveries in *Theope* (Harvey, 1987; DeVries *et al.*, 1994; DeVries and Hall, 1996; DeVries, 1997). However, still only eight *Theope* species (12%) are reported to have been reared (listed in Table 7 with a summary of their known hostplants and attending ant symbionts), and not a single complete life history has been published. With such a paucity of information, it is not possible at this stage to use morphological characters of early

Table 7. All reported rearings for the genus *Theope*, giving hostplants, attending ant symbionts, locations of rearings, and references. An asterisk preceeding a *Theope* species indicates that I have examined the reared voucher material (note that for some of these species the name differs from that given in the original publication - see text); numbers in parentheses represent the *Theope* species group. The definitions of plant families follow Gentry (1993).

Plant taxon	*Theope* taxon	Attending ant taxon	Location	Reference
EUPHORBIACEAE:				
Omphalea diandra	**virgilius* (X)	*Azteca* (Dolichoderinae)	Panama	(DeVries *et al.*, 1994)
LEGUMINOSAE:				
Inga sp.	**bacenis* (XI)	*Azteca* (Dolichoderinae)	Costa Rica	(DeVries *et al.*, 1994)
Inga sp.	*virgilius* (X)	*Azteca* (Dolichoderinae)	C. America	(DeVries, 1997)
Swartzia sp.	*virgilius* (X)	Unidentified	C. America	(Mallet *in* Harvey, 1987)
Cassia sp.	*publius publius* (XI)	*Azteca* (Dolichoderinae)	Costa Rica	(DeVries, 1997)
CONVULVULACEAE:				
Maripa panamensis	**lycaenina* (XIV)	*Azteca* (Dolichoderinae)	Panama	(DeVries *et al.*, 1994)
LECYTHIDACEAE:				
Gustavia superba	*lycaenina* (XIV)	*Azteca* (Dolichoderinae)	Panama	(DeVries *et al.*, 1994)
STERCULIACEAE:				
Theobroma cacao	*foliorum* (XIV)	Unidentified	Trinidad	(Guppy, 1904)
Theobroma cacao	*eudocia* (VI)	Unidentified	Trinidad	(Guppy, 1904)
Theobroma cacao	*eudocia* (VI)	Unidentified	Trinidad	(Kirkpatrick, 1954)
CECROPIACEAE:				
Cecropia insignis	**guillaumei cecropia* (XIII)	*Solenopsis* (Myrmicinae)	Costa Rica	(DeVries *et al.*, 1994)
BOMBACACEAE:				
Pseudobombax septenatum	**archimedes zyzyxoxyx* (IV)	*Dolichoderus* (Dolichoderinae)	Panama	(DeVries *et al.*, 1994)

stages to make any rigorous phylogenetic inferences, especially since only five of the fourteen *Theope* species groups are represented among the reared species. Certain meaningful patterns are nonetheless evident, and it is clear that a wealth of new character information would eventually be generated if a substantial number of species could be reared.

Theope larvae utilise a remarkable range of unrelated hostplants, and there are almost as many hostplant families (seven) recorded as there are reared *Theope* species. Among riodinid genera whose species have been reared, such a hostplant breadth is only seen elsewhere in *Emesis* Fabricius, 1807, *Juditha* Hemming, 1934, and *Synargis* Hübner, [1819] (Guppy, 1904; Kaye, 1921; Jørgensen, 1922; Zikán, 1953; Kirkpatrick, 1954; Barcant, 1970; Hayward, 1973; Kendall, 1976; Biezanko *et al.*, 1978; Callaghan, 1982, 1986b; Harvey, 1987; Gara and Onore, 1989; DeVries *et al.*, 1994; DeVries, 1997; Diniz and Morais, 1997). The evolution of this phenomenon in myrmecophilous genera is typically ascribed to their obligate associations with specific ant genera or families, in which the symbiotic relationship is so strong that females tend to use the presence of these ants instead of the plant as an oviposition stimulus (Pierce, 1983; Fiedler, 1991; DeVries, 1997). This can amply be said of *Theope*, which has a strong obligate association with dolichoderine ants, particularly of the genus *Azteca* (Harvey, 1987; DeVries *et al.*, 1994). The degree of host specificity for particular species or species groups is unclear at present, but it is apparent that at least some species are polyphagous on more than one plant family and that species of the monophyletic "*virgilius* + *terambus* group" commonly utilise plants in the Leguminosae.

Like ninety-nine percent of the known Lepidoptera (Strong *et al.*, 1984), all known *Theope* larvae are phytophagous and most feed on leaf matter, although *T. lycaenina* has been recorded feeding on flower parts (DeVries *et al.*, 1994), a behavior common in the

Lycaenidae (e.g. Chew and Robbins, 1984) but very rare in the Riodinidae, except in the genus *Eurybia* Illiger, 1807 (Harvey, 1987; DeVries *et al.*, 1994); at least one species, *T. archimedes*, is also known to drink both extrafloral nectar and homopteran honeydew, suggesting the potential importance of such secretions in the diet of *Theope* larvae (DeVries *et al.*, 1994). However, the adults of a few *Theope* species, most notably plesiomorphic species such as *T. eurygonina*, *T. tetrastigma* and *T. azurea*, exhibit greasiness of the wings, as seen in several other nymphidiine genera. Since this phenomenon is so pervasive in the genus *Setabis* whose only reared species, *S. lagus* (Cramer, 1777), has been found feeding on ant-attended membracid, jassid and coccid homopterans (Urich in Kaye, 1921; DeVries *et al.*, 1994), and aphytophagy is only known to have evolved from myrmecophily (Ehrlich and Raven, 1965; Cottrell, 1984; Pierce, 1995), it has been hypothesised that greasiness of the wings is correlated with carnivory (Hall and Willmott, 1995b; DeVries, 1997). The distinct possibility thus remains that greasy-winged *Theope* species are similarly carnivorous, either on homopterans or ant larvae, and that this phenomenon is considerably more widespread in the Nymphidiini than previously thought, as it is in certain myrmecophilous lycaenid groups, such as the subfamily Miletinae (Cottrell, 1984; Maschwitz *et al.*, 1988; Pierce, 1995).

Immature stages

Life history details, including descriptions of egg, larval and pupal morphology are given in each relevant species account, but an overview is also given here. The known eggs of *Theope* species are dorso-ventrally compressed, with a large, flat micropylar area and net-like sculpturing around the sides (see SEM illustrations in DeVries (1997)). They are laid singly or occasionally in small clusters on vigorously growing new shoots, although there is some reason to believe that a few species may oviposit directly on homopterans (see above), always in the presence of ants and/or near ants nests, and the resulting caterpillars are thus solitary or, more rarely, semi-gregarious (DeVries *et al.*, 1994; DeVries, 1997).

Most *Theope* larvae, of all instars, are a mottled green or brownish-green, but notable exceptions are *T. guillaumei* and *T. archimedes*, which are gray and maroon, and black and white respectively, and all have broad anal plates, well developed ventro-lateral flanges and lateral setae of variable length on all body segments (DeVries, 1997). All *Theope* larvae possess a number of "ant-organs", whose distribution among the two myrmecophilous riodinid tribes, namely the Nymphidiini (which contains the Lemoniini of Harvey, 1987 - see the "Taxonomy" section and Chapter 1) and Eurybiini Reuter, 1897 (*sensu* Harvey, 1987), is variable. Tube-like paired tentacle nectary organs (TNOs) (*sensu* Cottrell, 1984) on abdominal segment eight, which secrete nutritionally rich droplets to be harvested by ants (DeVries, 1988; DeVries and Baker, 1989), are present in both tribes (Harvey, 1987); SEM illustrations of the TNOs of *T. bacenis* (as *T. eleutho*) are given in DeVries (1997). Setose paired anterior tentacle organs (ATOs) (*sensu* Cottrell, 1984) on thoracic segment three, which influence ant behavior through the use of semiochemicals (DeVries, 1988, 1991a), were recorded in all lemoniadine and nymphidiine larvae studied by Harvey (1987), including *Theope*. However, ATOs are very difficult to discern and dissection of the larva is typically required to confirm their presence, and it seems that Harvey (1987) was mistaken in recording their presence in *Theope*, since DeVries and Poinar (1997), after carefully comparing the larvae of *Nymphidium* and *Theope*, concluded that ATOs were present in the former but absent in the latter, at least in the four species of *Theope* examined.

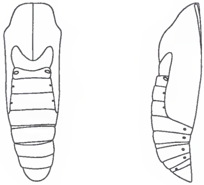
Unique to the Nymphidiini (all subtribes) (DeVries, 1997) is a pair of stridulatory rod-like appendages on the first thoracic segment that were first noted by Bruch (1926) and named vibratory papillae by Ross (1964a). As the head of the caterpillar moves in and out, the ribbed papillae grate against epicranial granulations to produce an acoustical call that is thought to function in attracting their ant-symbionts (Ross, 1966; DeVries, 1988, 1990, 1991b). A wave-form recording of the call for *T. lycaenina* is illustrated by DeVries (1997). Although variable in number, most caterpillars, including those of *Theope*, have two club-shaped vibratory papillae, but one of the reared species, *T. archimedes*, has two tri-pronged papillae (DeVries, 1991b, 1997). The morphology of these stridulatory structures is otherwise known to vary only subtly intergenerically; the vibratory papillae of *Theope* larvae have ribs of varying widths at the distal one-third, with the cusps directed in either an anterior or posterior direction, and the epicranial granulations are raised and pointed with heavy buttressing at the posterior edge (DeVries, 1997).

The last ant-organs relevant here are the bladder or balloon setae, a corona of inflated setae on the first thoracic segment that were first noted by Guppy (1904) in *T. eudocia* and *T. foliorum* from Trinidad (see Fig. 9). These setae are currently thought to be unique to the nymphidiine subtribes Nymphidiiti and Theopeiti and, although certain to be more widespread in these groups, have only thus far been reported to occur in *Nymphidium* and *Theope* (Harvey, 1987; DeVries, 1997). Similar setae occur in the tribe Helicopini (*sensu* Hall, 1998b), but these are yellow or white instead of dark colored, differ in fine structural details and are believed to have been evolved independently (Harvey, 1987; Hall, 1998b). The most extreme development of nymphidiine balloon setae is to be found in *Theope*, where exaggeratedly large clusters typically contain bulbous setae of differing sizes and colors. Very little is known about the morphology and function of these arresting structures but DeVries (1997) reports that they are resiliently turgid and covered with flat, overlapping scales, and that ants antennate the balloon setae and occasionally seize them in their mandibles; they subsequently move about in an agitated state, one which is transmitted to other nearby ants, suggesting that the chemical released may be acting as an ant alarm pheromone analogue to confer protection on the caterpillar.

The presence of pronounced balloon setae, along with the absence of ATOs, on a fossilised riodinid caterpillar discovered in a piece of Dominican amber is the main evidence that has led DeVries and Poinar (1997) to suggest that the caterpillar is a *Theope* species. This may be the case, but given the dearth of knowledge about nymphidiine caterpillars, including close relatives of *Theope* such as *Archaeonympha* (Hall and Harvey, 1998), it would seem to me almost equally likely that it does not belong to *Theope*. Generic determinations aside, at the very least this exciting discovery of the first fossilised riodinid caterpillar indicates that myrmecophilous nymphidiine riodinids were extant at least 15 to 20 million years ago (Iturralde-Vinent and MacPhee, 1996) and that they once inhabited the West Indies, where now only a single non-myrmecophilous species, *Dianesia carteri* (Holland, 1902) (*incertae sedis* section (4 FRV) of Harvey (1987)), exists (Riley, 1975; Harvey and Clench, 1980; Smith *et al.*, 1994). It is worth noting that the oldest West Indian riodinid fossil, also found in Dominican amber, is an adult specimen closely allied to the genus *Napaea* Hübner, [1819] (*incertae sedis* section (5 FRV) of Harvey (1987)) that has been estimated at approximately 25 million years old (DeVries, 1997). The oldest known riodinid fossil, *Riodinella nympha* Durden & Rose, 1978, was collected in the Green River Shale of Colorado in North America and dated to 48 million years old in the middle Eocene. This specimen, together with other fossilised papilionid and satyrine nymphalid specimens collected at the same site, currently represents the earliest undoubted occurrence of butterflies in the fossil record (Durden and Rose, 1978; Emmel *et al.*, 1992).

As can be seen from Table 7, *Theope* larvae have predominantly been found in association with dolichoderine ants, particularly those in the genus *Azteca*, which tenaciously attend them from the third instar onwards, when the caterpillars acquire their myrmecophilous organs. The only known exception is *T. guillaumei*, which appears to have made a secondary shift from the *Azteca* ants common on its hostplant, *Cecropia*, to the myrmicine *Solenopsis* ants that form small colonies at the leaf bases (DeVries *et al.*, 1994; DeVries and Hall, 1996). Both of these ant genera are secretion foragers, or trophobionts (*sensu* Wasmann), that form large and long-lived societies, and are thus typical of those known to associate with myrmecophilous caterpillars (Hölldobler and Wilson, 1990; DeVries, 1991a; Fiedler, 1991). The result of constant ant-attendance is greatly enhanced protection against arthropod predators (Pierce, 1987; DeVries, 1988, 1991b), so it is thus not too surprising, especially given the scant number of rearing records, that no parasitoids of *Theope* larvae have yet been recorded, but likely parasitoids are tachinid flies (DeVries, 1997). Pupation typically takes place in a curled leaf that has been fixed with silk, and one species, *T. lycaenina*, is even covered with a thin layer of carton constructed by its ant symbionts; all known *Theope* pupae are a uniformly cryptic brown or green color, smoothly cylindrical and unadorned with any processes (see Fig. 7) (DeVries, 1997). Note in Figure 7 the pattern of abdominal spiracular positions typical of early stage and adult nymphidiines, with the spiracle on segment one positioned dorsally and the remainder positioned ventrally.

Fig. 7. Dorsal (left) and lateral (right) views of a Costa Rican *Theope bacenis* pupa (material provided by P. DeVries).



Theope Doubleday, 1847

Theope Doubleday, 1847. *List. Spec. Lep. Ins. Brit. Mus.* 2: 6. Type-species by selection by Scudder (1875): *Polyommatus terambus* Godart, [1824], *Ency. méth.* 9 (Ins.) (2): 676.

= ***Parnes*** Westwood, 1851. In: Doubleday, E., *Gen. Diurn. Lep.* 2: pl. 73, fig. 3. Type-species by monotypy: *Parnes nycteis* Westwood, 1851, *op. cit.*. **[n. syn.]**

= ***Dinoplotis*** Stichel, 1911. In: Wytsman, J., *Gen. Insectorum* 112B: 293. Type-species by original description: *Dinoplotis orphana* Stichel, 1911, *op. cit.*: pl. 27, fig. 78. **[n. syn.]**

GROUP I: "*nycteis* group"

Theope nycteis (Westwood, 1851) **[n. comb.]**

Figs. 10a-f; 78; 145; 213; 261.

Parnes nycteis Westwood, 1851. In: Doubleday, *Gen. Diurn. Lep.* 2: pl. 73, fig. 3. **TL**: Pará, E. Brazil. Syntype male BMNH [Examined].

Identification and Taxonomy: Average forewing length: male 10mm, female 9mm.

Sexes similar but female has enlarged black spots in the apices of both ventral wing surfaces and a more rounded wing shape. *T. nycteis* is very similar to *T. brevignoni* but is most readily distinguished by having a different pattern of white pupils in the black apical spot of the VHW; in *T. nycteis* both white spots are centrally positioned whereas in *T. brevignoni* both are positioned along the proximal edge of a slightly enlarged and more circular black spot.

The ventral pattern of *T. nycteis* is geographically somewhat variable in the size and shape of the black spots on the VHW, the extent of marginal yellow on both ventral wing surfaces and the spacing of the yellow streaking. Specimens from west of the Andes appear to consistently have a more broken, mottled ventral pattern but insufficient material is available to establish whether taxonomic recognition of such a phenotype is warranted. The male genitalia of these two phenotypes do not differ significantly. Conversely, two of six dissected Amazonian males have slightly more pointed valvae and a small projection from the lower posterior corner of the last abdominal tergite, but there are no visibly discernible wing pattern differences and for the moment I can only ascribe these differences to variation. A very few Amazonian specimens also have rusty orange-brown at the base of both dorsal wing surfaces.

Note that all three members of the "*nycteis* group" have, until this work, been treated in the genus *Parnes*, but their morphology clearly places them in *Theope* (see the introductory "Taxonomy" section).

Biology: *T. nycteis* occurs up to 1000m in moist primary forest habitats. Its habits are typical of those species formerly included in the genus *Parnes*. Small groups of males are encountered locally on shaded hilltops where they fly incessantly around the base of tree trunks, often palm trees, within 1 or 2 meters of the ground. They fly slowly but with a rapid wing beat, rarely landing, in the early morning from about 0830 to 1000h and again, more commonly, in the afternoon from about 1330 to 1545h. Females are either found in male perching areas or along forest edges and in light gaps around mid-day. The fine-grained yellow ventral banding of *T. nycteis* and *T. brevignoni*, referred to by Nijhout (1991) as a "ripple" pattern, is common in the nymphalid butterfly subfamiles Brassolinae and Satyrinae, but very rare elsewhere. As all of these taxa are largely denizens of the gloomy understory, it is assumed that such disruptive patterning aids in camouflage when the butterfly is at rest.

Distribution: This species ranges from Costa Rica to the Amazon basin and the Guianas, and also occurs on the island of Trinidad. The single record of *T. nycteis* from central-west Argentina in the BMNH needs verification as it seems unlikely that appropriate tropical forest habitat stretches that far south; the species is not listed by Hayward (1973) for that country but then again neither are undoubtedly reliable Argentinian riodinid records such as *T. terambus*. Salazar (1995) reports *T. nycteis* from the upper Putumayo region of southern Colombia. The following additional localities are listed by DeVries (1997) for COSTA RICA: *Heredia*, Chilamate; *Puntarenas*, Ruta 2, 9.2 km S.E. of Chacarita; *Limón*, Hcda. Tapezco.

Specimens Examined: 53M 31F

PANAMA: *Chiriquí*, No specific locality 2M ZMHU; *Panamá*, 5 mi. N. of El Llano 4M, 5F USNM; *Colón*, Sta. Rita 1M USNM; *Canal Zone*, Colón 1F USNM; *Darién*, Caña 1M USNM. **VENEZUELA**: *Amazonas*, San Carlos 1M USNM; Cerro de la Neblina 1F USNM. **COLOMBIA**: *Cundinamarca*, Cananche 1M BMNH; *Meta*, Río Negro 2M USNM; *Caquetá*, Río Bodoquero 1M USNM. **ECUADOR**: *Esmeraldas*, La Punta, Lita-San Lorenzo rd. (Jun) 1M JHKW; El Durango (Sept) 1F JHKW; *Carchi*, Lita, ridge to east of Río Baboso (Jul) 1M JHKW; *Imbabura*, Paramba 1F BMNH; *Manabí*, Cerro Pata de Pájaro (Aug) 2M JHKW; *Pastaza*, Shell-Mera rd. 1M AME; km 35 Puyo-Tena rd. (Oct) 1F JHKW; *Napo*, Apuya (Aug) 3M, 1F JHKW; No locality data 1M BMNH. **PERU**: *Loreto*, Balsapuerto 1M AMNH; *Huánuco*, Pozuzo 1M BMNH. **ARGENTINA**: *La Rioja*, La Rioja 1M BMNH. **BRAZIL**: *Amazonas*, Ega 1M, 1F BMNH; Manaus 1M ZMHU; Maués 1M ZMHU; Massauary 1M ZMHU; *Rondônia*, nr. Cacaulândia 1M USNM; *Pará*, Santarem 1M, 1F BMNH; Rio Tapajós 1M, 1F BMNH; Itaituba-Obidos 1F BMNH; Pará 1M, 1F BMNH; Igarapé-Açu 1M AMNH; Amazon 3F BMNH; *Mato Grosso*, Diamantino 3M, 1F USNM; *Rio de Janeiro*, Paneiras 1M BMNH. **GUYANA**: *Upper Takutu/Upper Essequibo*, Annai, Essequibo river 1M, 2F BMNH; Essequibo river 1F AME; *Cuyuni/Mazaruni*, Roraima 1M, 1F BMNH; Quonga 1M BMNH; *East*

Berbice/Courantyne, Camp Jaguar, New River Triangle 2F AME; ? 6 mi. S. of Willepura 1M USNM. **SURINAM**: *Para*, Bersaba 1M ZMHU; No locality data 1M BMNH. **FRENCH GUIANA**: *Cayenne*, Goudronville, Riviere Kourou 1F BMNH; Route de L'est 2M USNM; Montsinéry 1F USNM; Saint-Elie 1M, 1F USNM; Fourgassie 1M USNM; *Saint Laurent du Maroni*, Saint Laurent du Maroni 1M BMNH; Saül 1M, 2F USNM; No locality data 1M BMNH. **TRINIDAD**: Tunapuna 1M AME. No locality data 1M BMNH; 1M ZMHU.

Theope brevignoni (Gallard, 1996) **[n. comb.]**

Figs. 11a,b; 79; 146; 261.

Parnes brevignoni Gallard, 1996. *Lambillionea* 96: 45-46, figs. 9, 10. **TL**: Montagne de Kaw, PK26, Roura, French Guiana. Holotype male MNHN and allotype female in coll. of L. & C. Brévignon, Guadaloupe; type illustrations [Examined].

Identification and Taxonomy: Average forewing length: male 10mm, female 8mm.

From the type illustrations, the sexes can be seen to be similar but the female has a more rounded wing shape. *T. brevignoni* is very similar to *T. nycteis* but differs most markedly by having the white pupils of the apical black spot on the VHW positioned proximally instead of centrally. The valvae of the male genitalia are broader than those of *T. nycteis* and have a small projection from the lower edge.

Biology: This species is the rarest in the "*nycteis* group". Its habits are similar to those of *T. nycteis* and it similarly occurs up to 1050m in moist primary forest. Gallard (1996) reports finding this species on hilltops in the early afternoon around 1330h, and in Ecuador a single male was similarly found hilltopping at about 1430h. G. Lamas (pers. comm.) reports that the Peruvian female was also encountered on a hilltop.

Distribution: This species is currently only recorded from Ecuador, Peru and the Guianas, but it clearly has a broader Amazonian distribution. In the original description, Gallard (1996) gives the following additional locality data for 10 males and 1 female from FRENCH GUIANA: *Cayenne*, Montagne de Kaw, Montagnes des Chevaux, Sinnamary; *Saint Laurent du Maroni*, Saül; G. Lamas (pers. comm.) reports the following additional locality data for a female from PERU: *Puno*, Zona Reservada Tambopata-Candamo, Río Tavara.

Specimens Examined: 5M

ECUADOR: *Pastaza*, km 32 Puyo-Macas rd. (Oct) 1M GWB; *Napo,* Finca San Carlo (Feb) 1M JHKW; Río Jondachi (1000m) 1M USNM; No locality data 1M BMNH. **GUYANA**: *Cuyuni/Mazaruni*, Bartica 1M BMNH.

Theope philotes (Westwood, 1851) **[n. comb.]**

Figs. 2d; 12a-d; 80; 147; 214; 261.

Parnes philotes Westwood, 1851. In: Doubleday, *Gen. Diurn. Lep.* 2: 464. **TL**: Pará, E. Brazil. Syntype male BMNH [Examined].

Identification and Taxonomy: Average forewing length: male 11mm, female 10.5mm.

Sexes similar but female has a paler, more uniformly shaded ventral surface and a more rounded wing shape. *T. philotes* is slightly larger than *T. nycteis* and *T. brevignoni* and has a very finely mottled yellow and brown ventral surface with prominent yellow discal cell end markings and no other transverse lines; the marginal, and especially apical, black spots of the ventral surface are also more prominent and the white pupils slightly larger.

Biology: The habits and habitat of *T. philotes* are similar to those of *T. nycteis*, although the species has been recorded flying slightly later in the morning, from 0850 to 1000h.

Distribution: *T. philotes* has a broad Amazonian and Guianan range. The following additional localities are listed by Lamas *et al.* (1991) for PERU: *Loreto*, Castaña, Arcadia.

Specimens Examined: 67M 33F

COLOMBIA: *Meta*, Río Negro 1M, 3F USNM; No specific locality 1M, 3F USNM; *Caquetá*, Río Bodoquero 2M USNM; *Amazonas*, Loretoyacu 1M AMNH. **ECUADOR**: *Sucumbíos,* Lumbaqui 1M USNM; *Napo,* Limoncocha 2M, 1F USNM; Campo Auca, Coca-Tiguino rd. (Apr) 1M JHKW; Finca San Carlo (Sept) 1M JHKW; Apuya (Feb, Aug) 2M JHKW; *Pastaza,* Sarayacu 1M, 1F BMNH. **PERU**: *Loreto*, Explornapo 2M AME; *Amazonas*, Río Santiago 2M, 1F AMNH; Achinamiza 2F AMNH; *Madre de Dios*, 50 km W.S.W. of Puerto Maldonado 1M, 1F USNM; *Puno*, Chaquimayo 4M BMNH; No locality data 1M AMNH. **BRAZIL**: *Amazonas*, São Paulo de Olivença 1F ZMHU; Ega 1M, 1F BMNH; 1M ZMHU; 1F AME; Maués 1M ZMHU; Massauary 1M ZMHU; *Rondônia*, nr. Cacaulândia 6M USNM; *Pará*, Obidos 2M, 2F ZMHU; Rio Tapajós 1M, 1F BMNH; Pará 3M, 3F BMNH; 1M, 1F ZMHU; Igarapé-Açu 1M AMNH; Amazon 4M, 1F BMNH. No locality data 3M, 2F BMNH. **GUYANA**: *Cuyuni/Mazaruni*, Kamakusa 1M AMNH; *East Berbice/Courantyne*, Camp Jaguar, New River Triangle 2F AME. **SURINAM**: *Brokopondo*, Berg en Dal 1F BMNH; *Para*, Bersaba 2F ZMHU; No locality data 1F BMNH; 2M ZMHU. **FRENCH GUIANA**: *Cayenne*, Cayenne 4M BMNH; 1M ZMHU; Galion 1M USNM; Saint-Elie 1M, 2F USNM; *Saint Laurent du Maroni*, Saint Laurent du Maroni 1M BMNH; 1M AME; No locality data 5M, 2F BMNH; 1M ZMHU.

GROUP II: "*tetrastigma* group"

Theope tetrastigma Bates, 1868

Figs. 2a; 13a-d; 81; 148; 215; 261.

Theope tetrastigma Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 408. **TL**: Cuparí, Rio Tapajós, E. Brazil. Syntype male and female BMNH [Examined].

Identification and Taxonomy: Average forewing length: both sexes 10mm.

Sexes similar but female has a more rounded wing shape. *T. tetrastigma* perhaps superficially most closely resembles *T. philotes* but it differs from that species by having a unicolorous pale brown ventral ground color, more prominent ventral discal cell end markings and uniformly sized submarginal spots on both ventral wing surfaces that consist of a white ring with a black pupil instead of vice versa. The male genitalia of *T. tetrastigma* place it as a sister species to *T. orphana*, both species uniquely sharing an aedeagus that is shorter dorsally than ventrally, has only weakly sclerotised lateral portions towards the tip and contains a single long thin cornutus. *T. tetrastigma* is easily distinguished from *T. orphana* by its continuous line of submarginal spots on the VFW and more distally placed spots on the VHW, by lacking the more elaborate ventral discal cell end markings of *T. orphana* and also the yellow-brown shading in the apex of the VFW and over much of the VHW; the male genitalia differ most prominently in the shape of the uncus and valvae. Both *T. tetrastigma* and *T. orphana* have an unusual anterior indentation at the ventral margin of the last male tergite, a character shared only with *T. hypoleuca.*

Biology: *T. tetrastigma* is very rare in major collections and absent from most. However, in the eastern lowlands of Ecuador, I have found it to be locally not uncommon. Males are active in hilltop lightgaps between 1420 and 1630h where they fly rather slowly in the relative gloom of the forest understory about 1 to 2 meters above the ground, behaving in a similar manner to the previous three species of the "*nycteis* group". The females are more rarely encountered in the same microhabitat.

Distribution: *T. tetrastigma* has a broad range that extends from the base of the eastern Andes to the lower Amazon and Guianan regions. The following additional localities have been reported to me by K. Willmott (pers. comm.) from PERU: *Loreto*, Cerros de Contamana, El Indio (Sept) (MUSM).

Specimens Examined: 9M 3F

ECUADOR: *Napo,* Río Tiputini (Mar) 2M JHKW; Finca San Carlo (Feb, Apr) 2M, 1F JHKW; Apuya (Oct) 1M JHKW. **BRAZIL:** *Pará*, Cuparí, Rio Tapajós 1M, 1F BMNH. **FRENCH GUIANA**: *Cayenne*, Compté, pk. 35.5 2M, 1F USNM; Galion, Roura 1M USNM.

Theope orphana (Stichel, 1911) [n. comb.]

Figs. 2e; 14a,b; 82; 149; 261.

Dinoplotis orphana Stichel, 1911. *Gen. Insectorum.* 112(B): 293, pl. 27, fig. 28. **TL**: Massauary, C. Brazil. Holotype male ZMHU [Examined].

Identification and Taxonomy: Average forewing length: both sexes 11mm.

From a photograph provided by J.-Y. Gallard (pers. comm.), it is apparent that the female differs little from the figured male. The ventral pattern of *T. orphana* is reminiscent of those of *T. christiani* and *T. zostera* but these patterns are examples of atavistic convergence and *T. orphana* is actually the sister species to *T. tetrastigma.* It differs from that species as outlined in the previous species account.

The forewing venation of *T. orphana* is most unusual in having vein Sc completely fused with vein R1, the character used by Stichel (1911) to erect his monotypic genus *Dinoplotis*, shown here to be a synonym of *Theope* (see the introductory "Taxonomy" section).

Biology: Little has been published on the natural history of this species, but specimens in the USNM, collected by Robbins and Becker, bear labels saying "territorial behavior" and give times between 1605 and 1645h. The hilltop localities for these specimens suggest that, like *T. tetrastigma*, *T. orphana* is a hilltopping species. Brévignon and Gallard (1998c) remarkably report capturing a female of *T. orphana* at light at night on a hilltop at 0600h; this phenomenon has not been previously reported for *Theope* but is known to occur sporadically in the Riodinidae, especially in the genera *Sarota*, *Euselasia*, and *Caria* Hübner, [1823] (Miller, 1970b; Brown, 1993; Hall, 1998b). The Amazonian and Guianan localities for this species consist of wet rainforest but that in Minas Gerais, south-east Brazil, consists of a rather dry blend zone between the wetter coastal forest and drier cerrado vegetation of the interior (Brown and Mielke, 1968).

Distribution: This species appears to be restricted to the lower Amazon and Guianan regions and the eastern and south-eastern states of Brazil. The following additional localities are listed by Brévignon and Gallard (1998c) for FRENCH GUIANA: *Cayenne*, Macouria.

Specimens Examined: 5M

BRAZIL: *Amazonas*, Massauary 1M ZMHU; *Bahia*, Morro do Chapéu (1475m) (Apr) 3M USNM; *Minas Gerais*, Serra do Cipo (1250m) (Apr) 1M USNM.

GROUP III: "*hypoleuca* group"

Theope hypoleuca Bates, 1868

Figs. 15a-f; 83; 150; 262.

Theope hypoleuca Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 406. **TL**: Santarem, C. Brazil. Syntype male and female BMNH [Examined].

Identification and Taxonomy: Average forewing length: both sexes 12mm.

Sexes similar but female has slightly more rounded wings. *T. hypoleuca* can rapidly be distinguished from all similar "*foliorum* group" species except *T. batesi* by having no submarginal ventral spotting. It differs from the superficially very similar west Amazonian phenotype of *T. batesi* by its slightly larger size, slightly more rounded wing shape, more extensive semicircle of blue on the DFW, paler ventral ground color and by lacking the dark brown line at the very margin of both ventral wing surfaces that is characteristic of the "*foliorum* group". The male genitalia of the two species are spectacularly different, those of *T. hypoleuca* placing it in one of the most plesiomorphic groups of *Theope*. The distinctive up-turned point to the tip of the valvae in *T. hypoleuca* is reminiscent of members of the "*tetrastigma* group" but a consilience of characters places it closest to *T. simplicia* and *T. azurea*. It differs from the former by having blue on the DFW and from the similar male of the latter by its slightly larger size and more rounded wing shape, by having paler dorsal blue coloration that is not present above vein Rs on the hindwing and a paler gray-brown ventral ground color, and by exhibiting substantial differences in the shapes of the aedeagus and valvae of the male genitalia.

Biology: Little is known about the biology of this rare species. In Ecuador, a solitary male was encountered within 20cm of the ground in the forest understory at 1400h.

Distribution: *T. hypoleuca* has been recorded from disparate localities across much of the Amazon basin. Brown (1987) also reports it from the edge of the basin, in the Cuiabá region of Mato Grosso state in south-west Brazil.

Specimens Examined: 16M 1F

ECUADOR: *Napo,* Apuya (Sept) 1M JHKW. **PERU**: *Madre de Dios*, Parque Nacional del Manu, Pakitza 6M USNM; Río La Torre 1M DA. **BRAZIL**: *Amazonas*, Tefé 1M BMNH; *Rondônia*, environs of Fazenda Rancho Grande, nr. Cacaulândia 3M NSM; *Pará*, Juruti 1M ZMHU; Santarem 1M, 1F BMNH; Amazonas 1M BMNH; No locality data 1M BMNH.

Theope simplicia Bates, 1868

Figs. 16a-d; 84; 151; 216; 262.

Theope simplicia Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 406. **TL**: Pará, E. Brazil. Syntype male and female BMNH [Examined].

Identification and Taxonomy: Average forewing length: both sexes 10.5mm.

Sexes similar but female has slightly more rounded wings and sparser blue scaling at the costal margin of the DHW. *T. simplicia* superficially closely resembles sympatric specimens of *T. leucanthe* from the lower Amazon, at least on the dorsal surface, but it has a slightly more pointed wing shape and a dirty cream instead of white ventral surface that lacks submarginal spotting. The absence of these ventral spots can be used to superficially distinguish *T. simplicia* from all similar members of the "*foliorum* group", except *T. batesi.* The lack of an upper "arm" to the valvae of the male genitalia, whose presence characterises that group, places *T. simplicia* closest to *T. hypoleuca* and *T. azurea* from which it is most readily distinguished by lacking blue on the DFW. The male genitalia of *T. simplicia* are most similar in overall appearance to that of *T. azurea*, but the aedeagal tip is flared and opens to the left, and the vesica contains a number of sizeable sclerotised structures instead of a single scobinate patch.

Biology: Nothing is known about the biology of this species. Bates (1868), in the original description of *T. simplicia*, stated that it was common at the type locality of Pará, but his type series still constitutes the bulk of the known specimens, very few of which have been collected this century.

Distribution: *T. simplicia* is only known from the eastern and southern edges of the Brazilian Amazon.

Specimens Examined: 22M 4F

BRAZIL: *Pará*, Pará 8M, 2F BMNH; 1M, 1F ZMHU; Amazon 2M BMNH; *Mato Grosso*, Diamantino 1M USNM. No locality data 6M BMNH; 1M, 1F ZMHU; 3M MNHN.

Theope azurea Bates, 1868

Figs. 17a-d; 85; 152; 217; 262.

Theope azurea Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 406. **TL:** Fonte Boa, W. Brazil. Syntype male BMNH [Examined]; Lectotype male BMNH [Designated].

Identification and Taxonomy: Average forewing length: both sexes 10.5mm.

MALE: *T. azurea* is easily distinguished from similar "*foliorum* group" species by having a pale yellow ventral surface that lacks submarginal spots and by lacking an upper "arm" to the valvae of the male genitalia. The yellow ventral coloration that *T. azurea* shares with members of the "*pedias* group" appears to have been independently derived, and its closest relatives appear to be *T. simplicia* and *T. hypoleuca*. Although the wing pattern of *T. azurea* is more similar to that of *T. hypoleuca*, from which it is distinguished in that species account, the male genitalia are more similar to those of *T. simplicia*; *T. azurea* diagnostically has a single scobinate patch at the tip of the aedeagus.

FEMALE: the female of *T. azurea* has not been previously recognised and is figured here for the first time. It is diagnosed by a combination of having the same spotless pale yellow ventral surface as the male, blue on the DHW that is largely restricted to the anal half of the wing and blue on the DFW that forms a horizontal "V"-shape at the base of the wing in the discal cell and along the anal margin.

Although two type localities are given by Bates (1868) in the original description, there are no specimens of *T. azurea* in the BMNH from one of these, Ega, and only a single labelled syntype from the other, Fonteboa. Since there is therefore a possibility of a mixed type series for *T. azurea*, I designate as a lectotype the aforementioned labelled syntype in the BMNH. It bears the following labels: "azurea", "Theope/azurea./Bates./Godman-Salvin/Coll. 1914.-5.", "Fonteboa,/Amazons./Bates Coll.", "Type/H.T.".

Biology: In eastern Ecuador, I have encountered males of *T. azurea* as uncommon, solitary individuals along forested ridgetop trails throughout the early to mid afternoon from about 1300 to 1530h. Females are considerably rarer and only a handful are known in museum collections.

Distribution: *T. azurea* appears to be restricted to a narrow region of the western Amazon, no specimens having been collected in the very well sampled areas of Madre de Dios in Peru and Rondônia in Brazil, towards the south-west. A single historical record from Panama in the MNHN is certainly a labelling error given the disjunct range, the lack of recently collected specimens and the occasional occurrence of other undoubted mislabellings in the collection.

Specimens Examined: 52M 6F

VENEZUELA: *Amazonas*, San Carlos 2M, 1F USNM. **COLOMBIA**: *Cundinamarca*, Medina 1M JHKW; *Meta*, Villavicencio 1M, 1F JLC; *Guainía*, Santa Rosa 1M BMNH. **ECUADOR**: *Pastaza,* Sarayacu 1M BMNH; *Napo,* Yarina (Jul) 1M JHKW; Limoncocha 1M USNM; Jatun Sacha (Nov) 1M DA; Chichicorrumi (Feb, Sept) 2M JHKW; Finca San Carlo (Feb, Apr, Sept) 3M JHKW; Apuya (Oct) 1M JHKW; No locality data 3M BMNH. **PERU**: *Loreto*, Nauta 1M BMNH; Iquitos 1M BMNH; 10M, 3F MNHN; 1M AMNH; St. Roque, nr. Iquitos 2M AME; Explorama, 50 mi. N.E. of Iquitos 1M AME; Pebas 3M ZMHU; Caballo Cocho 1M BMNH; *San Martín*, Jepelacio 1M MNHN; Pumayacu 3M, 1F AMNH. **BRAZIL**: *Amazonas*, São Paulo de Olivença 1M BMNH; Tefé 1M BMNH; 4M MNHN; Fonte Boa 2M BMNH; Ipiranga 1M MNHN; Tomar 1M ZMHU. Mislabelled: Panama 1M MNHN.

GROUP IV: "*archimedes* group"

Theope archimedes (Fabricius, 1793)

Theope archimedes archimedes (Fabricius, 1793)

Figs. 2b; 18a-d; 86a; 153a; 218; 262.

Hesperia archimedes Fabricius, 1793. *Ent. Syst.* 3(1): 320; *Jones's Icones* pl. 36, fig. 4. **TL**: "Habitat in Indiis" [sic]. Types unknown; type illustrations [Examined].

= ***Theope thebais*** Hewitson, 1860. *Ill. Exot. Butts.* 2: 97, pl. 49, figs. 1, 4. **TL**: Amazon. Syntype male BMNH [Examined]. **[n. syn.]**

Identification and Taxonomy: Average forewing length: male 16mm, female 16.5mm.

Since its description, riodinid systematists have continually found it very difficult to classify the taxon *archimedes*, for very few authors, if any, can in fact have had much idea of what it really looked like. It was described in the genus *Hesperia* by Fabricius (1793) with the following curt Latin description that is far from sufficient for identification purposes (the square bracketed portion is mine): "alis integerrimis nigris: disco coeruleo, subtus fuscis immaculatis. Statura praecedentium [*Metacharis ptolomaeus*]. Alae omnes nigrae disco coeruleo, subtus omnes fuscae, immaculatae". Lavish color illustrations were made of many Fabricius types, including *archimedes*, by W. Jones (1783-[1785]), but only an original copy was made and it resides in relative obscurity in the Hope library at the Oxford University Museum in Oxford, England. Westwood (1851) was thus unable to place *archimedes* in any genus and it was Bates (1868) who, under the heading "species described by authors not at present determinable", first suggested that it was "probably a species of *Theope*". Stichel (1911, 1930) even erected the "Archimediformes" as one of the names for his *Theope* species groups for a curiously phylogenetically diverse group of species that included *archimedes*, at the same time stating that he believed *archimedes* to be a dubious species. Seitz (1920) suggested that it might be a form of *T. virgilius*. I have examined and I figure the original type illustration made by Jones (1783-[1785]). It certainly does resemble a *Theope* species, but the ventral surface lacks any tornal spots on the hindwing that might indicate conspecificity with *T. virgilius*. It somewhat resembles a female *T. thestias*, but there is no hint of yellow coloration at the base of the VFW. To my mind, the illustration most closely resembles a female *T. matuta* or the species that has universally been called *T. thebais*, but the lack of red at the base of the VFW and the probable capture localities of the Guianas or east Brazilian seaboard suggest it represents the latter, which I synonymise into *T. archimedes*.

It is probable that *T. archimedes* was described from a specimen in the collection of Dru Drury, which was sold at auction by King & Locheé in London in May 1805 (Chalmers-Hunt, 1976), and eventually, at least in part, reached the British museum through the Milne Collection (Zimsen, 1964). However, no type specimens for *T. archimedes* are now known to exist in the BMNH or any other museum. China, of the British Museum, states (in Zimsen, 1964): "It seems likely that the specimens from the Milne Collection were not marked as Drury types at the time, and have probably been eliminated from the collection as being bad specimens", but G. Lamas (MUSM, pers. comm.) suggests that certain specimens may never have reached the BMNH and there is instead a slight possibility that types of *T. archimedes* reside unrecognised in the Macleay collection in Sydney, Australia. Until such time as this possibility can be eliminated, I refrain from designating a neotype, but hope, for the sake of nomenclatural stability, that as first reviser, my taxonomic arrangement will be followed by future authors.

MALE: *T. archimedes* is only mistakable for *T. matuta*, the nominate of one species closely resembling that of the other. Characters that distinguish the two species, include the slightly smaller size of *T. archimedes*, its slightly more pointed wing shape, the blue in cell Cu2 of the DFW extending further towards the distal margin than that in the other forewing cells, the reduced amount of red at the base of the costa on the VFW, the less prominent discal cell end markings of the ventral surface, the virtual lack of dark brown streaks in the submargins of both ventral wing surfaces and the increased amount of pale gray ventral shading, especially distally. The male and female genitalia of the two species do not differ. An interesting series of three males collected by D. Ahrenholz (pers. comm.) at the base of the eastern Andes in Ecuador exhibit several wing pattern characters intermediate between nominotypical *archimedes* and the subspecies *zyzyxoxyx*. This suggests either that there is some gene flow along the eastern Andes from the nearest known population of typical *zyzyxoxyx* at Villavicencio in east Colombia or that these pattern elements represent atavistic aberrations.

FEMALE: females are more difficult to identify, but the size, wing shape and ventral pattern characters as outlined above do permit separation (but note that red at the base of the VFW is more extensive in females). The dorsal coloration of *T. archimedes* also tends to be less greenish.

Biology: This species appears to be most frequently encountered in forest edge and secondary forest habitats, where R. Busby (pers. comm.) reports both sexes visiting flowering bushes.

Distribution: The nominate subspecies has a broad Amazonian and Guianan distribution where it is the only representative of the species group.

Specimens Examined: 33M 13F

VENEZUELA: *Bolívar*, Suapure 1F MCZ; *Amazonas*, San Carlos 1F USNM. **ECUADOR**: *Napo,* Misahualli (Nov) 1M DA; km 4 Misahualli-Puerto Napo rd. (Oct) 3M RCB; 1F GWB; Puerto Napo (Oct) 1M RCB; km 4 Tena-Pano rd. (Sept) 2M DA; No locality data 1M BMNH. **PERU**: *Loreto*, Iquitos 1F MNHN; *Madre de Dios*, 5 km N.E. of Shintuya 1F AME. **BRAZIL**: *Amazonas*, Tefé 1M AME; *Rondônia*, environs of Fazenda Rancho Grande, nr. Cacaulândia 2F NSM; *Pará*, Villa Nova 1M BMNH; Rio Tapajós 2M, 2F BMNH; Itaituba 1M BMNH; 4M, 1F ZMHU; Santarem 1F BMNH; Pará 1M, 1F BMNH; Amazon 3M BMNH; No locality data 2M BMNH; 2M ZMHU. **GUYANA**: *Potaro/Siparuni*, Potaro river 1M AME. **FRENCH GUIANA**: *Cayenne*, Pte. de Kaw 1M USNM; pk. 20 Kaw 2M USNM; Cacao 3M USNM; *Saint Laurent du Maroni*, Saint Laurent du Maroni 1F MNHN. No locality data 1M MNHN.

Theope archimedes zyzyxoxyx D'Abrera, 1994 **[n. stat.]**

Figs. 18e-h; 86b; 153b; 262.

Theope zyzyxoxyx D'Abrera, 1994. *Butts. Neotropical Region, Part VI*: 1002, figs. **TL**: Colombia. Holotype male BMNH [Examined].

Identification and Taxonomy: Average forewing length: male 16mm, female 16.5mm.

MALE: This subspecies differs most noticeably from the nominate by having pale gray-white coloration in the basal costal region of the DHW and increased blue on the DFW that extends postdiscally. In these respects, the taxon *zyzyxoxyx* very closely resembles the sympatric *T. matuta heureka* (described below), but all of the specific distinguishing characters for the two species outlined in the nominate account above still pertain here. It is for this reason and the parapatry of *zyzyxoxyx* and *archimedes* that I place the former, which was described as a full species by D'Abrera (1994), as a subspecies of *T. archimedes*.

FEMALE: the female is distinguished from those of similar taxa, especially the sympatric *T. matuta heureka*, by contrasting the ventral patterns as outlined previously for males.

Biology: DeVries (1997) reports observing the males of this subspecies in Panama perching in lightgaps high in the forest canopy or along forest edges and females in similar microhabitats around mid-day, but lower to the ground at other times. Both sexes visit the flowers of *Tetrathylacium* and *Serjania* vines in the canopy.

An examination of reared voucher material indicates that the foodplant *Pseudobombax septenatum* (Bombacaceae), first reported by DeVries *et al.* (1994) under the name

"*Theope* nr. *matuta*" is referrable to *T. archimedes zyzyxoxyx*. The white egg is heavily sculptured along the sides and has a flat micropylar area. It is laid in small clusters of two to six and the resultant early instar larvae are semi-gregarious; unusually, the larvae are tended by the dolichoderine ant *Dolichoderus bipsinosus* (DeVries *et al.*, 1994). The mature caterpillar is also unusual and the most phenotypically divergent of all known *Theope* larva. It has a shiny black head capsule with a conspicuous corona of dark purple balloon setae on the prothoracic shield, and the unusual trait of bearing a pair of tri-pronged vibratory papillae; the velvety black body is covered with inverted V-shapes on the dorsum of each segment that are outlined in white, has reddish brown lines at the posterior edge of segments A2 and A3 that are interrupted at A4 and then present again along segments A5 and A6, a purplish pink ventral surface that is conspicuous the full length of the body on lateral areas above the legs, and a well developed black anal plate with distal margins trimmed with purplish pink. The pupa, which is roundly cylindrical and uniformly brown, as in other congeners, is formed inside the partially rolled edge of a leaf (DeVries, 1997). DeVries (1997) should be consulted for SEM's of the eggs and larval vibratory papillae, and black and white drawings of the mature larva and pupa.

Distribution: This subspecies is currently known from Costa Rica to Colombia and north Venezuela, but it probably also occurs in north-west Ecuador. Most specimens from Colombia originate from central and western regions, but it is not unexpected to have also a record from Villavicencio, in the north-eastern Andes, as many west Andean butterfly taxa range this far. The following additional localities are listed by DeVries (1997) (as *T. matuta*) for COSTA RICA: *Puntarenas*, Sirena.

Specimens Examined: 48M 25F

PANAMA: *Canal Zone*, Piña 6M, 6F AME; 5M, 5F USNM; 1M FSCA; Colón 1M, 1F USNM; Gamboa 4M USNM; 9M, 2F AME; Gatun 7M, 6F USNM; Cocoli 1M USNM; Barro Colorado Is. 2M AMNH; *Darién*, Caña 1M, 1F USNM; Cerro Pirre 1F USNM; No locality data 1M AME. **VENEZUELA**: *Carabobo*, Las Quiguas, San Esteban Valley 2M, 1F BMNH. **COLOMBIA**: *Antioquia*, Victoria (2400ft) 1F USNM; Casabe, across Río Magdalena from Barranca Bermejo 2M AME; 2M AMNH; *Cundinamarca*, Bogotá 1M BMNH; *Caldas*, No specific locality 1F USNM; *Meta*, Villavicencio 1M MNHN; No locality data 1M BMNH; 1M MNHN.

Theope matuta Godman & Salvin, 1897 [**stat. rev.**]

Theope matuta matuta Godman & Salvin, 1897

Figs. 19a-d; 87a; 154a; 219; 262.

Theope matuta Godman & Salvin, 1897. *Trans. ent. Soc. Lond.* 45(2): 246. **TL**: Santa Clara Valley (1200ft), Costa Rica. Holotype female BMNH [Examined].

Identification and Taxonomy: Average forewing length: male 17.5mm, female 18mm.

MALE: *T. matuta* can only be confused with its sister species *T. archimedes*. Characters that distinguish it include its larger size, slightly less pointed wing shape, even distal edge to the blue of the DFW, greater amount of red at the base of the costa on the VFW, and the presence of dark brown streaks in the submargins of both ventral wing surfaces.

FEMALE: the female may be identified by matching the ventral surface pattern with that of the male.

The taxon *matuta* was described by Godman and Salvin (1897) as a full species from a single female specimen, but subsequently treated as a subspecies of *T. thebais* by Stichel (1911, 1930). The full elaboration in this work of the constituent taxa in the "*archimedes* group" and their respective geographic ranges shows two quite phenotypically distinct species to be broadly sympatric and I thus officially return *matuta* to the rank of species.

Biology: This is the most poorly represented taxon of the "*archimedes* group" in collections. In Costa Rica, DeVries (1997) reports observing males perching in forest canopy lightgaps and along forest edges and females similarly at canopy level around mid-day, but closer to the ground at other times. Both sexes are reported to feed on the flowers of *Tetrathylacium* and *Serjania*.

Distribution: The nominate subspecies is restricted to Costa Rica and Panama. The following additional localities are listed by DeVries (1997) (as *T. thebais*) for COSTA RICA: *Heredia*, Chilamate, Finca La Selva; *Puntarenas*, Sirena.

Specimens Examined: 9M 4F

COSTA RICA: *Cartago*, Tuis 1F BMNH; Turrialba 1M USNM; *Limón*, Santa Clara Valley 1F BMNH. **PANAMA**: *Panamá*, El Llano 3M, 2F USNM; *Canal Zone*, Gatun 4M USNM; Piña 1M USNM.

Theope matuta heureka Hall, **new subsp.**

Figs. 19e-h; 87b; 154b; 262.

Description: MALE: forewing length 17.5mm. Forewing costa slightly convex in basal half, hindwing pointed at tornus. *Dorsal surface*: forewing ground color black; basal triangle of blue occupies three-quarters of cells above and below cell Cu2, half of cell Cu1 and a third of cell M3, distal margin of these cells being straight, entire discal cell and small portions at base of cells M2-Rs, distal margin of these cells being uneven; discal cell end marked with a thick black line, all veins outlined in black. Hindwing ground color black, brown at apex, pale brown at anal margin; blue occupies all of cells Cu2-M3, except for an increasingly broad black margin, entire discal cell, basal three-quarters of cell M2, basal third of cells M1 and Rs and basal half of cell Sc+R1; blue in upper half of discal cell and above vein M2 paler; discal cell end weakly marked with thin black line, all veins outlined in black. *Ventral surface*: forewing ground color brown; all veins outlined in dark brown, horizontal dark brown line through middle of discal cell and cell Cu2; base of costa red, remainder dark brown; discal cell end marked with thick dark brown line, broad, diffuse dark brown band immediately distal, dark brown postmedial band extends vertically from anal margin to vein M3 then thickens and curves inwards to costa; a faint dark brown streak at submargin of cells Cu1-Rs, two in cell Cu2, with paler brown circles at proximal end faintly discernible. Hindwing differs from forewing by lacking red at base of costa and by having a paler dark brown discal band that extends between discal cell end and costa. *Head*: Labial palpi a mixture of dark brown and pale brown scales. Eyes bare and brown, margins brown. Frons dark brown edged with cream. Antennae black with white ventral scaling gradually decreasing from base to tip, entire inner edge bare brown; clubs black, tips orange-brown. *Body*: Dorsal surface of thorax and abdomen black, ventral surface brown, thin medial white line along ventral surface of abdomen. All legs brown. *Genitalia* (Figs. 87b; 152b): tegumen triangular; uncus with sharply pointed lower projection; falci long and thin; valvae roundly elongate with basal lateral bulge; aedeagus of even width with rounded tip; last tergite an approximate square with no posterior projections; last sternite with small rounded posterior projection that is produced into small points laterally and invaginated to connect with base of valvae.

FEMALE: differs from male in following ways: forewing length 18mm. Distal margins of both wings rounded. *Dorsal surface*: ground color of both wings pale brown; blue coloration paler, greenish and slightly reduced on both wings, especially postdiscally on forewing and in anal cells of hindwing. *Ventral surface*: all markings paler on both wings.

Types: *Holotype male*: COLOMBIA.- *Cundinamarca*, Bogotá; in the BMNH.

Allotype female: COLOMBIA.- *Cundinamarca*, Cananche, 1 Sept 1900 (M. de Mathan); in the BMNH. *Paratypes*: COLOMBIA.- 3 males: same data as AT. 1 male: *Cundinamarca*, Bogotá, 1918 (Frere Apolinaire-Marie). 1 male and 1 female: *Tolima*, Río Chili, Apr/Jun 1921. 1 female: *Boyacá*, Muzo, 10 Nov 1877 (O. Thieme); all in the BMNH. ECUADOR.- *Esmeraldas*, km 44 Lita-San Lorenzo rd., La Punta, 21 Jun 1994 (J. P. W. Hall); in the coll. of JHKW.

Etymology: The word "heureka", meaning "I have found it" in Greek, alludes to the exclamation of delight supposedly given by Archimedes in the bath when he realised how to test the purity of Hiero's crown.

Diagnosis: Seitz (1920) referred to this taxon under Bang-Haas's manuscript name "*gloriosa*"; however, since it was never published, it becomes a nomen nudum, necessitating the description herein. *T. matuta heureka* subsp. n. differs from the nominate by having increased blue on the DFW that occupies the entire discal cell and extends further towards the distal margin in all other cells, with postdiscal blue appearing in cells M2 to Rs, increased blue on the DHW, including a paler portion in the basal costal region, and by having a more uniformly paler brown ventral surface without such strongly contrasted paler elements. This subspecies most closely resembles the broadly sympatric *T. archimedes zyzyxoxyx* but it is readily distinguished by the specific characters highlighted in the account of nominate *T. matuta*. The male genitalia of all four taxa do not differ nor, based on examination of the nominate taxa, are the female genitalia expected to differ.

Biology: In Ecuador, a solitary male was found perching atop vegetation about 6 meters above the ground in a hilltop lightgap at 1500h.

Distribution: This taxon occurs in central and western Colombia and in north-west Ecuador.

Specimens Examined: 50M 6F

COLOMBIA: *Chocó*, Río San Juan 1M ZMHU; *Antioquia*, Medellín 2M AME; *Cundinamarca*, Bogotá 15M, 1F BMNH; 1M USNM; 4M MNHN; Cananche 3M, 1F BMNH; *Tolima*, Río Chili 1M, 1F BMNH; Magdalena 2M ZMHU; *Boyacá*, Muzo 1F BMNH; 7M MNHN; ? Caucathal 1M MNHN; No locality data 1M, 1F BMNH; 3M, 1F ZMHU; 2M MNHN; 4M, 1F AMNH. **ECUADOR**: *Esmeraldas,* La Punta (Jun) 1M JHKW. No locality data 1M BMNH; 1M MNHN.

GROUP V: "*pedias* group"

Theope pseudopedias Hall, **new sp.**

Figs. 20a-d; 88; 155; 220; 263.

Description: MALE: forewing length 12mm. Distal and costal margins of forewing convex, hindwing elliptical with roundly pointed apex. *Dorsal surface*: forewing ground color black; pale blue semicircle in basal two-thirds of wing occupies all but a broad black distal border in cells above and below vein 1A+2A, three-quarters of cell Cu1, half of cell M3, distal margin of these cells being evenly diagonal, entire discal cell, half of cell M2 and very basal portions of cells M1 and Rs. Hindwing ground color pale blue; very thin distal black margin expands slightly at apex, costal margin brown, anal margin gray. *Ventral surface*: both wings entirely pale yellow except for paler coloration at anal margin of forewing with some black scaling at base of wing (typically concealed by hindwing). *Head*: Labial palpi a mixture of brown and yellow scales. Eyes brown and bare, margins yellow. Frons yellow with brown scales through middle. Antennae of HT missing; those of PT black with ventral white scaling that decreases from base to tip, inner edge bare and brown; clubs black, tips orange brown. *Body*: Dorsal surface of thorax and abdomen black, ventral surface pale brown. All legs yellow-brown. *Genitalia* (Figs. 88; 153): tegumen and uncus compact, distal margin of uncus concave; falci small and compact; valvae roughly rectangular with basal lateral bulge; aedeagus pointed at tip, distal portion of vesica studded with tiny sclerotised structures; last tergite an approximate square with no posterior projections; last sternite with a small roundly pointed posterior projection that is produced into small points laterally and invaginated to connect with the base of the valvae.

FEMALE: does not differ externally from the male in any significant regard. *Genitalia* (Fig. 220): corpus bursae oblong, sclerotised and invaginated signae triangular in lateral view, elongate and ovoid in dorsal view; ductus bursae very long and twisted, attached to ostium bursae by sclerotised plate that is raised at edges; ductus seminalis broad at base and studded with tiny sclerotised structures, narrows abruptly and is then only lightly sclerotised; ostium bursae an elongate, sclerotised circle.

Types: *Holotype male*: GUATEMALA.- *Izabal*, Cayuga (Schaus & Barnes); in the USNM.

Allotype female: same data as HT; in the USNM. *Paratypes*: 1 female: same data as HT, May; in the BMNH. MEXICO.- *Veracruz*, Presidio: 1 female: Jun 1942 (T. Escalante); 1

female: Jun 1954 (T. Escalante); both in the AME. COSTA RICA.- *Heredia*, Chilamate: 1 female: Dec (P. J. DeVries); in the coll of PJD.

Etymology: The name of this species refers to its great similarity to the sympatric congener *T. pedias*.

Diagnosis: *T. pseudopedias* n. sp. is phenotypically very similar to and has always been confused with *T. pedias*. However, the striking difference between the two species is that the sexes of *T. pseudopedias* are monomorphic. Despite this, the male and female genitalia of the two species do not differ. The male is only just barely separable from that of sympatric *T. pedias*, which has a paler ventral yellow ground color than most South American males, but can be distinguished by its smaller size, slightly paler blue dorsal coloration and much thinner black border at the distal margin of the DHW, especially in the apex. The identical female, however, does not at all resemble that of *T. pedias*, instead more closely resembling Central American females of *T. mundula*; it differs from that species by its smaller size, more rounded wing shape, by having a larger semicircular blue patch on the DFW, essentially no black border at the distal margin of the DHW and typically black scaling at the base of the VFW.

Biology: Nothing substantive is known about the biology of this species since in all prior literature and in collections, it has been confounded with its sympatric sibling congener *T. pedias* and often referred to as *T. pedias isia* (see below). Label data indicate that it flies in at least the months of May, June and December.

Distribution: This species is currently known to occur from southern Mexico to central Costa Rica and is likely to also occur in Panama. The following additional locality is listed by Austin *et al.* (1996) (as *T. pedias* - but see Fig. 15 in that work) for GUATEMALA: *El Petén*, Tikal.

Specimens Examined: 2M 7F

MEXICO: *Veracruz*, Presidio 1F USNM; 2F (Jun) AME. **GUATEMALA**: *Izabal*, Cayuga 1M, 1F USNM; 1F (May) BMNH. **COSTA RICA**: *Cartago*, Juan Viñas (Jun) 1M, 1F USNM; *Heredia*, Chilamate (Dec) 1F PJD.

Theope pedias Herrich-Schäffer, [1853]

Figs. 2f,g; 21a-f; 89; 156; 221; 263.

Theope pedias Herrich-Schäffer, [1853]. *Samml. Neuer. aussereurop. Schmett.* 1: 55, pl. 11, figs. 24, 25. **TL**: Surinam. Syntype male SMNS; type photograph [Examined, courtesy of G. Lamas].

= ***Theope thelpusa*** Hewitson, 1860. *Ill. Exot. Butts.* 2: 98, pl. 49, figs. 7, 8. **TL**: Amazon. Syntype female BMNH [Examined].

= ***Theope hypoxanthe*** Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 405. **TL**: Pará, E. Brazil. Syntype male and female BMNH [Examined]; Lectotype male BMNH [Designated].

= ***Theope isia*** Godman & Salvin, 1878. *Proc. zool. Soc. Lond.* 1878(2): 368. **TL**: Polochic Valley, Guatemala. Syntype male BMNH [Examined]. **[n. syn.]**

Identification and Taxonomy: Average forewing length: both sexes 14mm.

MALE: although of variable hue, the ventral yellow of *T. pedias* is never brilliantly glossy as it is in certain superficially similar species of the "*sericea* group", such as *T. sericea*, *T. dabrerai* and *T. galionicus*, nor does it ever approach the rich orange of its closer relatives *T. pepo* and *T. devriesi*. The most similar of these, *T. devriesi*, additionally differs from *T. pedias* by having reduced blue on the DFW and male genitalia with different aedeagus and valve shapes. The sister species of *T. pedias*, which has indistinguishable male genitalia, is *T. pseudopedias* (described above), and although their respective females are easy to tell apart, the males are certainly not, especially those from sympatric Central American populations. The two most obvious characters separating male *T. pedias* from male *T. pseudopedias* are its noticeably larger size and the presence of a small black area in the apex of the DHW.

FEMALE: the dorsal surface of this sex is most distinctive and the forewing pattern, with its small area of basal blue divided from three or four blue postdiscal rays by a black discal cell end line, and tornal black rays that often occur on the otherwise entirely blue hindwing are both unique within the genus. The forewing pattern elements also tend to be violaceous while the hindwing is a glossy blue.

Several synonyms of *T. pedias* have been described. Understandably deceived by the marked sexual dimorphism in this species, Hewitson (1860) described the first of these, *thelpusa*, from a female specimen. The second, *hypoxanthe*, was described by Bates (1868) from male and female specimens. Unfortunately, the syntype female is not conspecific with the male, instead representing female *T. mundula*, thus erroneously fostering the belief that *hypoxanthe* and *pedias* were two sibling species whose males were essentially inseparable but whose females were quite different; it is a belief that is still reflected in the arrangements of certain older museum collections. It is therefore necessary to designate the male syntype as a lectotype. This specimen in the BMNH bears the following labels: "hypoxanthe", "B.C.A. Lep. Rhop./Theope/hypoxanthe,/Bates./Godman-Salvin/Coll. 1914.-5.", "Para,/L. Amazons./H.W. Bates.", "Type/H.T.". Finally, the taxon *isia* was described as a full species by Godman and Salvin (1878), from a Central American male, on the basis that its ventral surface was "a paler and purer yellow", but it was downgraded to the rank of subspecies by Stichel (1911). Although Central American specimens of *T. pedias* do tend to have slightly paler yellow ventral ground colors, the difference is marginal, and given the variability of this character throughout the range of the species, I also treat *isia* as a synonym of *T. pedias*.

It should be noted that a specimen of *T. pedias* labelled as a type in the ZMHU, like other Herrich-Schäffer riodinid "types" in that museum, is falsely labelled, and that the true type resides in the SMNS (G. Lamas, pers. comm.).

Biology: *T. pedias* typically occurs from sea-level to 1000m, but has been collected as high as 1500m, and is predominantly associated with wet forest habitats. It is one of the most commonly represented *Theope* species in collections, probably because both sexes frequent open forest trails, forest edges and secondary growth areas. Males may be encountered perching in such areas, especially in the vicinity of streams, during the afternoon from about 1200 to 1300h. DeVries (1997) reports this species feeding on the small white flowers of various plants in open pastures.

Distribution: *T. pedias* is one of the most wide-ranging *Theope* species, occurring from central Mexico, throughout Central America, to the Guianas and the Amazon basin, and the island of Trinidad. Hoffmann (1940) additionally reports the ocurrence of this species in the Mexican states of Guerrero and Oaxaca, although these records may well apply to *T. pseudopedias*. The following additional localities are listed by Warren *et al.* (1998) (identification not certain) for MEXICO: *Colima*, Agua Dulce; by DeVries (1997) for COSTA RICA: *Heredia*, Finca La Selva; *Puntarenas*, Rincon de Osa; and by Lamas *et al.* (1991) for PERU: *Loreto*, Castaña..

Specimens Examined: 289M 121F

MEXICO: *Veracruz*, Atoyac 1M BMNH; Presidio 4M AMNH; 6M AME; Tezonapa 1M AME. **GUATEMALA**: *Izabal*, Cayuga 2M USNM; *Alta Verapaz*, Río Polochic Valley 1M BMNH. **HONDURAS**: *Atlántida*, 18 km W. of Le Ceiba 1M USNM.

COSTA RICA: *Cartago*, Turrialba 1M, 1F AME; *Heredia*, Puerto Viejo 1M USNM; *Alajuela*, San Mateo 1F USNM; *Puntarenas*, Golfito 1F USNM; 7 km N.E. of Las Alturas 1M AMNH. **PANAMA**: *Chiriquí*, Bugaba 2M BMNH; *Canal Zone*, Gatun 3F USNM; Piña 3F FSCA; 2M, 4F AME; 2M USNM; La Pita 1M, 1F USNM; Río Torti 6M, 3F USNM; Madden Forest 1F USNM; Cocoli 2M, 1F USNM; No specific locality 2M, 5F USNM; *Veraguas*, Santa Fe 1M USNM; *Darién*, Caña 1F USNM; No locality data 2F FSCA; 1M MNHN. **VENEZUELA**: *Carabobo*, Las Quiguas, San Esteban Valley 1F BMNH; *Monagas*, Caripito 1M AMNH; *Bolívar*, Suapure 1M MCZ; *Amazonas*, Río Mavaca 1F AMNH; Cerro de la Neblina 1M USNM. **COLOMBIA**: *Valle de Cauca*, Río Tatabro 1F JS; *Cundinamarca*, Bogotá 1F BMNH; *Santander*, El Centro 1F AMNH; *Putumayo*, Florida 1M MNHN; Puerto Umbria 1M, 1F MNHN; *Amazonas*, Río Tacana 1M AMNH; No locality data 1F BMNH; 1M ZMHU. **ECUADOR**: *Cañar*, Angas 1F AME; *Sucumbíos*, Garzacocha, La Selva 4M PJD; *Napo*, Limoncocha 6M, 1F USNM; km 4 Misahualli-Puerto Napo rd. (Oct) 2M, 1F RCB; Puerto Napo (Oct) 1F RCB; 1F DA; Archidona 1M USNM; Finca San Carlo (Feb) 1F JHKW; Apuya (Feb, Aug, Oct) 3M JHKW; 1F RCB; 1M GWB; Pimpilala (Feb) 1M JHKW; *Pastaza*, Sarayacu 1M BMNH; Canelos 1M BMNH; 32 km S. of Puyo (Oct) 1M RCB; *Morona-Santiago*, Bomboiza (Jul) 1M JHKW; *Zamora-Chinchipe*, Zumbi 1M AMNH; No locality data 5M, 2F BMNH. **PERU**: *Loreto*, Contamana 1M BMNH; Iquitos 1M BMNH; 1M ZMHU; 2M, 1F MNHN; 1M AME; Pebas 1M BMNH; Caballo Cocho 2M BMNH; Río Sucusari, Explornapo-Aceer 2M, 1F USNM; Balsapuerto 1F AMNH; N.E. Peru 1F AMNH; *Amazonas*, Río Santiago 1M AMNH; Achinamiza 3M, 1F AMNH; *San Martín*, Pumayacu 1F AMNH; *Huánuco*, Río Pachitea 1M MNHN; *Pasco*, Río Chucharras, Río Palcazu (320m) 1F BMNH; *Madre de Dios*, Erika 1F USNM; Parque Nacional del Manu, Pakitza 21M, 7F USNM. **BOLIVIA**: *La Paz*, Río Songo 1F ZMHU;

1M MNHN; No specific locality 1M ZMHU. **BRAZIL**: *Amazonas*, Tefé 8M BMNH; 1M ZMHU; 2M, 1F MNHN; São Paulo de Olivença 1M BMNH; Tonantins 1M BMNH; Río Juruá 1F BMNH; Humaitá 2M, 1F BMNH; Maués 2M, 1F MNHN; 1M MZC; Manaus 1M MNHN; Manicoré 2M MNHN; Ipiranga 2M MNHN; Río Negro 1M AMNH; *Rondônia*, environs of Fazenda Rancho Grande, nr. Cacaulândia 42M, 10F NSM; 1M USNM; *Pará*, Obidos 1M ZMHU; Rio Tapajós 1M, 1F BMNH; 1M MNHN; Santarem 2F BMNH; Itaituba 1F MNHN; Cuiabá-Santarem highway 1M USNM; 2M, 1F ZMHU; Pará 5M BMNH; Igarapé-Açu 1M, 1F AMNH; 1F AME; Amazon 2M, 2F BMNH; 1F ZMHU; 4M, 1F MNHN; *Maranháo*, Montes Aureos 1M, 3F BMNH; *Bahia*, Itabuna 1M BMNH; 1M AME; Rio Mucuri, Mucuri 5M, 1F USNM; No specific locality 1M ZMHU; *Espírito Santo*, Linhares 35M, 9F AME; No specific locality 1F BMNH; *Mato Grosso*, Cuiába 1M BMNH; Diamantino 7M, 2F USNM; *Minas Gerais*, 1F Leopoldina ZMHU; No locality data 1M BMNH; 1F USNM. **GUYANA**: *Upper Demerara/Berbice*, Demerara river 1M BMNH; *Cuyuni/Mazaruni*, junction of Cuyuni and Arimu rivers 1M USNM; Kartabo, Bartica 1M USNM; 1M AME; Carimang river 1M, 4F BMNH. **SURINAM**: No locality data 1F BMNH; 1M ZMHU. **FRENCH GUIANA**: *Cayenne*, Cayenne 7M BMNH; 1F USNM; Montsinéry 2M USNM; Kaw 2F JHKW; *Saint Laurent du Maroni*, Saint Laurent du Maroni 1M, 1F BMNH; 3M MNHN; No locality data 3M, 4F BMNH. **TRINIDAD**: St. Annes 1M AME; No locality data 1M BMNH; 2M, 1F AME. No locality data 9M, 2F BMNH; 3M, 3F ZMHU; 1M, 1F MNHN; 1M AMNH.

Theope devriesi Hall & Willmott, 1996

Figs. 22a-d; 90; 157; 222; 263.

Theope devriesi Hall & Willmott, 1996. *Trop. Lepid.* 7(1): 64-65, figs. 2a-d. **TL:** Guapiles, Costa Rica. Holotype male BMNH and allotype female FSCA [Examined].

Identification and Taxonomy: Average forewing length: both sexes 14mm.

MALE: *T. devriesi* is readily distinguished from the widespread *T. pedias*, especially sympatric Central American specimens, by having dorsal coloration that is more of a pure blue than blue-purple, restricted to a more basal area of the forewing and leaves a relatively wide black distal margin on the hindwing, especially at the apex, and by its darker orange ventral coloration. Male genitalic differences also exist in the shape of the valvae and aedeagus, and the last sternite is larger. The unusual ventral color of *T. devriesi* is only shared by *T. pepo*, but the males of the latter species are instantly recognised by the purple squares around the distal margin of the DFW.

FEMALE: differs from *T. pedias* by lacking postdiscal blue rays on the DFW and by having a darker ventral surface as in the male, and from *T. pepo* by having a black distal margin to the DHW and, again, no postdiscal blue on the DFW.

Biology: *T. devriesi* is rare throughout its range. In Ecuador, a single female was found feeding on a large streamside flowering tree near Lita in the company of its sibling congener *T. pepo*. Specimens have been collected in most months of the year.

Distribution: *T. devriesi* occurs from Mexico to western Ecuador. I have not examined any specimens from Mexico, but de la Maza (1987) illustrates a male (as *T. pedias isia*) from Chajul, Mexico.

Specimens Examined: 3M 9F

GUATEMALA: *Izabal*, Cayuga 1F USNM. **COSTA RICA**: *Limón*, Guapiles 1M BMNH. **PANAMA**: *Panamá*, El Llano 1F USNM; *Canal Zone*, Madden Forest 1M USNM; Colón 1F FSCA; Piña 1F AME; 1F USNM; La Pita 1M USNM; Gatun 1F

USNM; Cocoli 1F USNM; *Darién*, Caña 1F USNM. **ECUADOR**: *Carchi*, nr. Lita, Río Baboso (Jul) 1F JHKW.

Theope pepo Willmott & Hall, 1994

Figs. 23a-d; 91; 158; 223; 263.

Theope pepo Willmott & Hall, 1994. *Trop. Lepid.* 5(2): 87-89, figs. 3a-c. **TL**: Río Baboso, nr. Lita, W. Ecuador. Holotype male and allotype female to be deposited in the BMNH [Examined].

Identification and Taxonomy: Average forewing length: both sexes 17mm.

MALE: *T. pepo* shares its rich pumpkin orange ventral surface only with *T. devriesi* but is slightly larger than that species, has a more strongly convex forewing costa, uniquely positioned purple squares along the distal margin of the DFW that, with the distal region of the DHW, are a darker purple shade than the brighter basal blue of both wings, no black around the distal margin of the DHW, and more extensive dirty brown scaling around the distal margins of both ventral wings. The male genitalia of the two species differ most noticeably in the shape of the aedeagus, which in *T. pepo* is longer and tapers into a thinner, upwardly curved and pointed tip; *T. pepo* also has a longer last tergite and larger last sternite than all other species in the "*pedias* group".

FEMALE: at the time of the original description of *T. pepo*, the authors were unaware of the existence of the phenotypically similar, undescribed *T. devriesi*, and unfortunately a *T. devriesi* female was erroneously chosen and illustrated as the allotype of *T. pepo*, an error subsequently rectified by Hall and Willmott (1996a). The true female of *T. pepo*, like the male, also has more dirty brown shading around the distal margins of the ventral surface and no black margin on the DHW, but most noticeably always has more extensive, postdiscal blue on the DFW than *T. devriesi* that extends to the middle of the distal margin.

Biology: *T. pepo* is very rare in major collections, primarily because of its restricted range, but it can be locally not uncommon in appropriate microhabitats. It is known to occur from near sea-level to 900m and like most "*pedias* group" species, it appears to be almost exclusively encountered in association with riverside gallery forest or forest edge habitats. A large colony was encountered in Ecuador on the Río Baboso, near Lita, where several males were perching on a bush overhanging the river, opposite a flowering tree where both males and females were nectaring. The perching males made frequent rapid sorties out over the water before returning to rest beneath the same clump of leaves, the brilliant orange of their ventral wing surfaces, contrasted against the green leaves, being visible from quite some distance. A pair were found *in copulo* at 1400h beneath a leaf on the perching bush, but the species was active from 1200 to 1600h.

Distribution: This species is endemic to the Chocó region of west Ecuador and west Colombia. The following additional localities have been reported to me by K. Willmott (pers. comm.) from COLOMBIA: *Valle de Cauca*, Río Tatabro; *Risaralda*, Santa Cecilia (LC, JS).

Specimens Examined: 7M 11F

COLOMBIA: *Chocó*, Río San Juan (Jun) 1M AME. **ECUADOR**: *Carchi*, nr. Lita, Río Baboso (Jul) 4M, 2F JHKW; *Imbabura,* Paramba 3F BMNH; *Pichincha,* Reserva Río Guaycuyacu (Jun) 1F JW; Tinalandia (May) 1F JHKW; 1M DA; Alluriquin 1F USNM; Río Toachi 1F USNM; *Bolívar*, La Chima 2F BMNH; No locality data 1M BMNH.

GROUP VI: "*eudocia* group"

Theope eudocia Westwood, 1851

Figs. 3j-l; 9; 24a-d; 92; 159; 224; 264.

Theope eudocia Westwood, 1851. *Gen. Diurn. Lep.* 2: 439. pl. 70, fig. 4. **TL**: Pará, E. Brazil. Syntype male BMNH [Examined].

= ***Theope eudocia pulchralis*** Stichel, 1910. *Berl. ent. Zeit.* 55(1/2): 86. **TL**: Colombia. Syntype male ZMHU [Examined]; Lectotype male ZMHU [Designated]. [**n. syn.**]

Identification and Taxonomy: Average forewing length: male 13.5mm, female 13mm.

MALE: *T. eudocia* is the sister species of *T. acosma* and together they form a most distinctive group that can be placed phylogenetically between the "*pedias*" and "*sericea* groups". *T. eudocia* is readily distinguished from *T. acosma* by having a variably sized arc of purple-blue in the apex of the DFW. The male genitalia of the two species do not differ.

FEMALE: the female, which lacks the blue apical patch on the DFW of the male, can often not be distinguished with certainty from that of *T. acosma* and the distribution of orange on the DFW must be matched as well as possible with sympatric male specimens. Females of *T. eudocia* tend to lack orange inbetween the discal cell and the forewing costa. The female genitalia of the two species do not differ.

T. eudocia is a geographically variable species in the extent of orange and purple-blue (in males) on the DFW, and the prominence of submarginal brown spots on the DHW. The taxon *pulchralis* was described as a subspecies of *T. eudocia*, but although the type has more orange on the DFW than that of *T. eudocia*, this character does not vary consistently with geographic region and I synonymise *pulchralis* with *T. eudocia*. In order to restrict the type locality of *pulchralis* to a single biogeographical region (it was described from Panama and Colombia), I designate the single syntype in the ZMHU as a lectotype. It bears the following labels: "pulchralis/Stich.", "Columbia/Kalbr.", "Type".

Biology: This species occurs from sea level up to about 1000m and is commonly represented in collections, no doubt because it is usually found in degraded forest habitats, along forest edges, streamsides and in second growth areas. Both sexes may be encountered from mid-morning, around 1000h, until about 1500h, one of the longest male activity periods of any *Theope* species. Both sexes have been found feeding on flowering bushes.

The foodplant and life history of *T. eudocia* were first reported and illustrated by Guppy (1904) (see Fig. 9) from Trinidad, but subsequently also reported by other authors (Guppy in Seitz, 1920; Kaye, 1921; Kirkpatrick, 1954; Barcant, 1970). The foodplant is given as *Theobroma cacao* (Sterculiaceae), but, as for *T. foliorum*, this identification perhaps needs modern confirmation, since cacao has mistakenly been given as the hostplant in other historical butterfly rearing records (see Young, 1986). Kirkpatrick (1954) reports that the mature larva has an apple green body with a darker dorsal stripe and is covered with tiny, mainly pale setae, which are much longer laterally. The prothorax has numerous, anteriorly projecting balloon setae of varying sizes that are predominantly black and brown but also of a paler color. The mesothorax has purplish subdorsal stripes, purple spots at the posterior margin of the first seven abdominal segments, and a purple dorsal stripe on segments seven to nine that expands laterally on segment eight to form a cross; the dorsum of segment nine is enlarged into a flat saddle that covers segment ten. Guppy (in Seitz, 1920) states that "The larva lies in a rolled-up leaf of the cocoa plant in the surroundings of which the ants of the guard build their paper nests; on trying to separate them from their larva, they appear very excited"; the attending ants have not been identified.

Distribution: *T. eudocia* is widespread throughout Central America and South America, occurring as far south as south-east Brazil, and is also found on the islands of Trinidad and Tobago. It should be looked for in northern Central America and southern Mexico. The following additional locality is listed by Lamas *et al.* (1991) for PERU: *Loreto*, Arcadia.

Specimens Examined: 176M 161F

HONDURAS: *Cortés*, La Cambre 1F BMNH. **NICARAGUA**: *Chontales*, No specific locality 2M, 3F BMNH; No locality data 1F BMNH. **COSTA RICA**: *Limón*, Limón 1M USNM; Banana River 2F USNM. **PANAMA**: *Bocas del Toro*, No specific locality 1F USNM; *Canal Zone*, Colón 2F USNM; Piña 5F AME; 1M, 1F USNM; *Panamá*, Altos de Pacora 2F USNM; Cerro Jefe 2F USNM; N. of El Llano 1M, 1F USNM; Cerro Campana 1M FSCA; 1M, 1F AME; No specific locality 1M FSCA; *Darién*, Caña 2M, 8F USNM. **VENEZUELA**: *Táchira*, Cucuta 1M, 1F USNM; *Barinas*, Río Caparo 1M USNM; *Aragua*, Rancho Grande 1F AMNH; *Carabobo*, Valencia 1M ZMHU; *Nueva Esparta*, Isla de Margarita 3M, 3F USNM; No locality data 2F BMNH. **COLOMBIA**: *Caldas*, Victoria 1F USNM; *Cundinamarca*, Cananche 1M BMNH; *Boyacá*, Muzo 1F MNHN; *Putumayo*, Mocoa 1F JHKW; Upper Putumayo 1F MNHN; *Meta*, Río Negro 1M BMNH; 4M MNHN; 1F USNM; No locality data 1M ZMHU; 1F MNHN. **ECUADOR**: *Esmeraldas,* La Punta, km 44 Lita-San Lorenzo rd. (Jul) 1F JHKW; *Carchi,* Lita, Río Baboso (Jul) 1M, 1F JHKW; *Pichincha,* Tinalandia (Jul, Oct) 1F FSCA; 1F AME; 1M GWB; Alluriquin 2M, 2F USNM; *El Oro,* Portovelo 1F AME; *Los Ríos,* Río Palenque 1M, 1F AME; *Bolívar,* Chimbo 1M, 1F BMNH; *Pastaza,* Sarayacu 1M BMNH; 32 km S. of Puyo (Oct) 1M GWB; 14 km S. of Shell (Oct) 1F RCB; *Napo,* Limoncocha 1M USNM; Las Minas, nr. Misahualli (Sept) 1M JHKW; km 4 Misahualli-Puerto Napo rd. (Oct) 1M, 1F RCB; 1F GWB; Chichicorrumi (Jul) 1M JHKW; Puerto

Napo (Oct) 1F RCB; Apuya (Oct) 1F RCB; *Sucumbíos,* Lumbaqui 1F USNM; No locality data 3M BMNH. **PERU**: *Loreto*, Iquitos 10M, 1F MNHN; St. Roque, nr. Iquitos 1M AME; Balsapuerto 1M AMNH; *San Martín*, Taropoto 1M BMNH; Pumayacu 2F AMNH; *Huánuco*, Tingo María 1F AME; *Pasco*, Río Chucharras, Río Palcazu (320m) 1F BMNH; *Madre de Dios*, nr. Puerto Maldonado 2M USNM; Parque Nacional del Manu, Pakitza 13M, 5F USNM; *Cuzco*, Qbda. Chaupmayo 1F AMNH; No locality data 1M BMNH; 1M MNHN; 1M USNM. **BOLIVIA**: No locality data 1M BMNH; 1F USNM. **BRAZIL**: *Amazonas,* São Paulo de Olivença 2M BMNH; 1F ZMHU; Humaitá 1F BMNH; Manicoré 3M MNHN; Tefé 1M MNHN; Ipiranga 5M, 1F MNHN; 4M, 1F AMNH; *Rondônia*, environs of Fazenda Rancho Grande, nr. Cacaulândia 14M, 13F NSM; *Pará*, Rio Tapajós 1M, 1F BMNH; 1M MNHN; Santarem 1M ZMHU; 2M, 1F ZMHU; Pará 2M, 1F BMNH; 1M ZMHU; 1M AME; Igarapé-Açu 1M AME; Amazon 1M, 3F BMNH; 1F ZMHU; *Goiás*, Santa Rita do Araguaia 1M, 3F USNM; *Paraiba*, João Pessoa 3M, 4F USNM; *Mato Grosso*, Cuiába 3F BMNH; 1M, 1F ZMHU; Diamantino 12M, 4F USNM; *Minas Gerais*, No specific locality 1F BMNH. **GUYANA**: *Upper Takutu/Upper Essequibo*, Annai, Essequibo river 1M, 2F BMNH; *Cuyuni/Mazaruni*, Carimang river 1M, 2M, 1F BMNH; Quonga 1F BMNH; No locality data 1M BMNH. **SURINAM**: No locality data 1M BMNH. **FRENCH GUIANA**: *Cayenne*, Cayenne 6M, 1F BMNH; 1M ZMHU; 2M, 2F MNHN; 4M, 6F USNM; Route de L'est 1M, 2F USNM; Galion, Roura 2M, 1F USNM; Compté 1F USNM; Goudronville, Riviere Kourou 1F BMNH; *Saint Laurent du Maroni*, Saint Laurent du Maroni 1M, 4F BMNH; 1M, 1F MNHN; No locality data 4M, 3F BMNH. **TRINIDAD**: Caparo 1M BMNH; St. Annes 1M, 3F BMNH; 3M, 4F MNHN; St. Georges 1M, 1F BMNH; Port of Spain 1M, 2F BMNH; 1M AME; 6 mi. N.W. of Arima 2M AME; 1M AMNH; Dabadie 1F AMNH; Tunapona 1M AME; 1F AMNH; Maracas Bay 1F AMNH;

Santa Cruz Valley 1M, 1F AMNH; Sangre Grande 1F AME; No locality data 1F BMNH; 1M, 1F AME; 2M, 2F AMNH. **TOBAGO**: No locality data 2F BMNH. No locality data 5M, 3F BMNH; 2M, 1F ZMHU; 1M MNHN.

Theope acosma Stichel, 1910 **[n. stat.]**

Figs. 25a-f; 93; 160; 225; 264.

Theope eudocia acosma Stichel, 1910. *Berl. ent. Zeit.* 55(1/2): 86. **TL**: São Paulo de Olivença, W. Brazil. Syntype male ZMHU [Examined].

Identification and Taxonomy: Average forewing length: male 13.5mm, female 13mm.

MALE: the taxon *acosma* was described as a subspecies of *T. eudocia* and its taxonomic status has been in question ever since (e.g. DeVries, 1997). Given the broad and yet far from comprehensive sympatry of the two phenotypes, the independent geographic variation of the two phenotypes and differences in their ecology (see below), I formally raise *acosma* to species status. *T. acosma* is readily distinguished from *T. eudocia* by lacking purple in the apex of the DFW.

FEMALE: the females of the two species are very difficult to distinguish with certainty, but those of *T. acosma* would appear to typically have an orange spot at the base of the costa of the DFW or an expanded area of orange between the discal cell and costa, as is often present in the male. Microhabitat capture location may also be relevant in identification (see below).

Central American specimens of *T. acosma* tend to have an enlarged area of orange on the DFW compared to Amazonian specimens, but there is insufficient material available to establish whether these represent only local populations (especially since they originate from higher altitudes around 1000m) or a geographically distinct subspecies. This pattern difference is particularly noticeable in males, such that the sexes are essentially monomorphic in these populations.

Biology: *T. acosma* occurs from near sea-level to about 1100m. It is much more poorly represented in collections than its sister species *T. eudocia*, in part because it has a smaller range, but also perhaps for the same ecological reasons that aid in distinguishing them as distinct species. Whilst *T. eudocia* is almost exclusively encountered at forest margins and in secondary growth habitats, it is my experience that *T. acosma* is similarly encountered in intact forest habitats. This is well exemplified at one locality in Ecuador, Apuya, where solitary individuals of *T. eudocia* may be found flying low to the ground along streamsides and in scrub areas around the edges of the forest block, whereas a small group of *T. acosma* males may be found perching in a particular hilltop lightgap within the forest block. They perched 3 to 5 meters above the ground and were consistently active between 1410 and 1545h each day, but solitary individuals were also rarely encountered in the vicinity around just before mid-day. Callaghan (1983) records males hilltopping in Villavicencio, Colombia, in the early morning from 0830 to 0920h, suggesting that, like members of the "*nycteis* group", this species has a bimodal pattern of perching times. A female was found in a fish-baited trap placed 15 meters above the ground in a forest lightgap at Apuya at 1545h, a rare phenomenon in the Nymphidiini (see introductory "Ecology" section).

Distribution: The currently known range of *T. acosma* is somewhat disjunct and includes Costa Rica, Panama and Guyana, and the west Amazon region. Callaghan (1983, 1985) reports this species from east Colombia, as does Salazar (1995) from the Putumayo region. Brown and Mielke (1967) report it from the planalto region of south-east Brazil and Brown (1987) reports it from Mato Grosso state in south Brazil; however, given the large range extension that these Brazilian records would represent and the possibility that they have been confused with the more common *T. eudocia*, these records needs verification. The following additional locality is listed by DeVries (1997) for COSTA RICA: *Heredia*, La Virgen de Sarapiqui.

Specimens Examined: 26M 6F

COSTA RICA: *Alajuela*, Miravalles 1M BMNH; *Puntarenas*, San Vito 1M USNM. **PANAMA**: *Chiriquí*, Potrerillos (3600ft) 2M, 1F USNM; 2F AME. **ECUADOR**: *Sucumbíos,* Garzacocha, La Selva 1M, 1F PJD; *Napo,* Río Napo 3M BMNH; Apuya (Oct) 5M, 2F JHKW; *Pastaza*, Pitirischa (Jul) 1M JHKW. **PERU**: *Loreto*, Iquitos 1M BMNH; 1M ZMHU; Caballo Cocho 1M BMNH; N.E. Peru 1M AMNH. **BRAZIL**: *Amazonas,* São Paulo de Olivença 2M BMNH; 1M ZMHU; Humaitá 2M BMNH; *Rondônia*, environs of Fazenda Rancho Grande, nr. Cacaulândia 1M NSM. **GUYANA**: *Upper Demerara/Berbice*, Malali 1M AMNH. No locality data 1M AMNH.

GROUP VII: "*sericea* group"

Theope excelsa Bates, 1868

Figs. 26a-d; 94; 161; 226; 265.

Theope excelsa Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 406. **TL**: Ega, W. Brazil. Syntype male BMNH [Examined].

Identification and Taxonomy: Average forewing length: male 18.5mm, female 17mm.

MALE: *T. excelsa* is a distinctive species, distinguished from Amazonian congeners by its large size, bulbous hindwing tornal shape, dull darkish yellow and often grainy ventral surface, and large apically directed triangle of blue on the DFW that leaves a broad and even black border at the distal and costal margins. *T. excelsa* would appear to be most closely related to the allopatric *T. kingi*, which has similar male genitalia, but differs by having more pointed hindwings, a darker yellow ventral surface and more blue than purple dorsal coloration that is more extensive on the DFW, extending postdiscally.

FEMALE: female *T. excelsa* has essentially the same dorsal pattern of the male, although it is pale purple, and is most readily distinguished from similar "*sericea* group" females by having purple immediately distal to the discal cell on the DFW.

Biology: *T. excelsa* occurs in intact wet forest habitats up to 1000m, and in eastern Ecuador I found it to be locally not uncommon. Solitary males were encountered perching under large leaves in hilltop and ridgetop lightgaps, typically high in the subcanopy but sometimes as low as 4 meters from the ground, from where they would make rapid sorties around the clearing before returning to rest beneath the same leaf. If one male was removed, another would soon take its place. They are active from about 1300 to 1515h.

Distribution: *T. excelsa* occurs throughout much of the Amazon basin, from the base of the eastern Andes to the Atlantic, into the Guianas and on the island of Trinidad. The following additional localities have been reported to me by G. Austin (pers. comm.) from BRAZIL: *Rondônia*, environs of Fazenda Rancho Grande, nr. Cacaulândia (NSM); and by K. Willmott (pers. comm.) from COLOMBIA.- *Meta*, Río Ariari (JS).

Specimens Examined: 62M 16F

VENEZUELA: *Bolívar*, Suapure 1M MCZ; *Delta Amacuro*, Río Aguirre 3F MNHN; *Amazonas*, Munduapo, Orinoco 1M BMNH. **ECUADOR**: *Pastaza*, 32 km S. of Puyo (Oct) 1M GWB; *Napo*, Limoncocha 1F USNM; Río Tiputini (Mar, Apr) 3M JHKW; Jatun Sacha (Nov) 1M DA; Apuya (Oct, Dec) 4M JHKW; km 30 Puyo-Canelos rd. (Oct) 1M JHKW; No locality data 2M BMNH. **PERU**: *Loreto*, Caballo Cocho 1M BMNH;

Iquitos 1M, 2F MNHN; Balsapuerto 1M AMNH; *San Martín*, Juanjuí 1M MNHN; Chazuta 4M MNHN; *Huánuco*, Monte Alegre, Río Pachitea 3M ZMHU; *Madre de Dios*, Erika 1M USNM; Parque Nacional del Manu, Pakitza 1M, 2F USNM. **BRAZIL**: *Amazonas*, Tefé 2M BMNH; 1F MNHN; Maués 1F ZMHU; 1F MNHN; Ipiranga 3M MNHN; Rio Umarí 1M MNHN; *Pará*, Pará 2F BMNH; No locality data 1M BMNH. **GUYANA**: No locality data 1F BMNH. **FRENCH GUIANA**: *Cayenne*, Mts. des Chevaux 1M USNM; Sinnamary 1M USNM; Galion 8M USNM; Route de L'est 8M USNM; Montsinéry 4M USNM; *Saint Laurent du Maroni*, Saint Laurent du Maroni 1M BMNH; 1F MNHN; 1M USNM; Saint Jean du Maroni 1M USNM. **TRINIDAD**: Rio Claro 1M AME; Sangre Grande 1M AME. No locality data 1M BMNH; 1F ZMHU.

Theope kingi Hall & Willmott, 1996

Figs. 27a-d; 95; 162; 227; 265.

Theope kingi Hall & Willmott, 1996. *Trop. Lepid.* 7(1): 63-65, figs. 1a-d. **TL**: Gatun, Canal Zone, Panama. Holotype male and allotype female USNM [Examined].

Identification and Taxonomy: Average forewing length: male 18.5mm, female 19mm.

Sexes similar but female has slightly more rounded wings, paler blue dorsal coloration and slightly paler yellow ventral coloration. *T. kingi* is a large species that most closely resembles the Amazonian *T. excelsa*. However, it has a broader wing shape, with more rounded hindwings that do not end in a bulbous tip at the tornus, a paler yellow ventral surface, and purple-blue rather than blue dorsal coloration (in the male) that is restricted to a much smaller area along the anal margin of the forewing and leaves the costal half of the discal cell on the hindwing black. The shape of the valvae of the male genitalia and last male sternite also differ between the two species. The female genitalia do not differ significantly, but from the single specimen dissected of each species, the signae of *T. kingi* appear to be more narrowly pointed.

Biology: The late G. B. Small and H. L. King are the only people to have collected this species and thus essentially no biological information is now available. *T. kingi* is clearly a very rare and/or localised inhabitant of wet lowland forest, as are all "*sericea* group" species, and it has only been collected in the months of February, June and July.

Distribution: *T. kingi* is currently only known from Panama, but it is certain to have a considerably broader range, as the neighbouring regions have been less well sampled. It is very likely to occur in the Chocó region of west Colombia and north-west Ecuador, but judging by material recently collected by R. Anderson in Nicaragua (in the AME), including *Archaeonympha smalli* Hall & Harvey, 1998, also known previously only from Panama (see Hall and Harvey, 1998), it may also prove to be present in Costa Rica and Nicaragua.

Specimens Examined: 5M, 4F

PANAMA: *Panamá*, 5 mi. N. of El Llano 2F USNM (Jun); *Canal Zone*, Piña 1M USNM (Feb); 1M, 1F (Jul) AME; Gatun 3M, 1F (Feb, Jun) USNM.

Theope barea Godman & Salvin, 1878

Figs. 2h,i; 28a-h; 96; 163; 228; 265.

Theope barea Godman & Salvin, 1878. *Proc. zool. Soc. Lond.* 1878(2): 369. **TL:** Veraguas, Panama. Syntype male BMNH and syntype female ZMHU [Examined]; Lectotype male BMNH [Designated].

= ***Theope caenina*** Godman & Salvin, 1878. *Proc. zool. Soc. Lond.* 1878(2): 369. **TL**: Veraguas and Chiriquí, Panama. Syntype male BMNH [Examined].

Identification and Taxonomy: Average forewing length: male 13mm, female 13.5mm.

MALE: the yellow ventral surface and pale brown postdiscal area of scaling on the DFW of *T. barea* mean that it can only be confused with *T. aureonitens* and *T. mundula*. It can quickly be distinguished from the former by having a much smaller area of pale brown scaling on the DFW, a more pointed wing shape, and a paler yellow ventral surface; the male genitalia of the two species are also quite different in the shape of the valvae and aedeagus, as are the last sternite and to a lesser extent the last tergite. Clearly, the sister species of *T. barea* is the very similar *T. mundula*. Both species are highly variable in size and wing pattern but *T. barea* can always be told apart by having blue only in the basal portion of the DFW and never in an inwardly curving arc around the distal submargin; blue is only ever present in DFW cell Cu1, if at all, as a small spot at the very cell base and never as a long dash. The male genitalia of the two species are also variable in the shape of the uncus, which either has one posteriorly projecting point or two, and the valvae, which are either rounded at the tip or have one or two tiny points, and unfortunately the two spheres of variation overlap to such an extent that there are no genitalic characters to consistently distinguish the two species.

FEMALE: *T. barea* has a more compact wing shape than *T. sericea* and blue on the DFW that never extends to the tornus; it is smaller than *T. excelsa* and has pale blue instead of pale purple dorsal coloration that does not extend postdiscally; it differs from the female of *T. galionicus* by having an inwardly diagonal distal margin to the blue of the DFW and a larger black area at the costal margin of the DHW without such a prominent black notch at the discal cell ends. The female of *T. barea* seems to be geographically variable, with certain specimens from Panama and all those from the Guianas having greatly reduced or even no blue on the DHW. In the Guianas, this character distinguishes female *T. barea* from female *T. mundula*. It is uncertain whether this phenotype occurs elsewhere in the Amazon basin (it has not yet been recorded), in which case it would be readily distinguishable from *T. mundula*, or whether it reverts to the Central American phenotype with blue on the hindwing, in which case it would be indistinguishable from sympatric females of *T. mundula*.

T. barea is seemingly a rather variable species in its size (FW length 12-15mm), wing shape (wings variably pointed), the shade of the ventral surface (pale yellow to a darker, dirty yellow), the exact shade of the dorsal blue coloration, and in how much blue there is at the very base of cell Cu1 of the DFW in males (there is a small blue area at the very base of cell Cu1 in Amazonian specimens). There is a slight possibility that I may be treating more than one sibling species here (the same can be said for *T. mundula*), but I can only maintain a single species until further information, including the collection of more material and perhaps molecular data, can be gathered that contradicts the arrangement presented here.

Godman and Salvin (1878) described the taxon *T. caenina* on the same page of the same work as *T. barea* and even from the same locality, diagnosing it on the basis that its ventral surface was "more ochraceous in tint, paler and not nearly so pure in tone". This spurious difference can be ascribed purely to the worn nature of the type specimen and, as explicitly stated by DeVries (1997), *T. caenina* is synonymous with *T. barea*.

Due to the difficulty in separating female *T. barea* and *T. mundula*, it seems prudent to designate the male syntype as a lectotype. This specimen in the BMNH bears the following labels: "B.C.A. Lep. Rhop./Theope/barea,/Bates./G.&S./Coll. 1914.-5.", "Veraguas,/Panama./Arce.", "Type./Sp. figured.", "Type/H.T.".

Biology: *T. barea* occurs from sea-level to about 1200m in a variety of forest habitats. In Ecuador, I have found solitary males perching in ridgetop and hilltop lightgaps between 1300 and 1430h, resting under leaves with their wings shut.

Distribution: *T. barea* is found from central Mexico through Central America into the Amazon basin. It is considerably more common in areas to the west of the Andes. The following additional localities are listed by Balcázar (1993) (as *T. pedias isia* - but see Fig. 22 in that work) for MEXICO: *Michoacán*, Pedernales; by DeVries (1997) for COSTA RICA: *Cartago*, Tuis; and are reported to me by C. Jiggins (pers. comm.) from ECUADOR: *Loja,* Tambo Negro.

Specimens Examined: 63M 23F

MEXICO: *Colima*, Colima, 1M AME; Comala 1F AME; *Guerrero*, No specific locality 1F USNM; *Morelos*, 10 mi. S. of Cuernavaca 1M AME; Huajintlan 1M AME. **NICARAGUA**: *Managua*, 15 km S. of Managua 1M, 1F AME. **COSTA RICA**: *Guanacaste*, Comelco, 8 km N.W. of Bagaces 1M USNM; *Alajuela*, Alajuela 1F USNM; *Heredia*, Finca La Selva, nr. Puerto Viejo 2M USNM. **PANAMA**: *Chiriquí*, Potrerillos (3600ft) 1F USNM; No specific locality 1M BMNH; 2M, 1F ZMHU; 3F MNHN; *Veraguas*, No specific locality 1M BMNH; *Panamá*, El Llano 1M, 1F USNM; Balboa 1M AMNH; *Colón*, 10 mi. W. of Portobelo 1F AME; *Canal Zone*, Los Ríos 3M FSCA; 2M AME; 20M, 1F USNM; Madden Dam 1F AME; Colón 1F AME; Curundu 1F DA; Paraiso 1M USNM; Gatun 1F USNM; 1F AME; Gamboa 1M USNM; 5M AME. **VENEZUELA**: *Aragua*, Puerto Cabello 1F ZMHU; *Amazonas*, Cerro de la Neblina 1F USNM. **COLOMBIA**: *Chocó*, San Pablo, Río San Juan 3M BMNH; 2M ZMHU; No locality data 1M USNM. **ECUADOR**: *Napo,* Finca San Carlo (Feb, Sept) 5M JHKW; *Pastaza,* Sarayacu 1M BMNH. **PERU**: *Madre de Dios*, Erika 1M USNM. **BRAZIL**:

Amazonas, São Paulo de Olivença 1M MNHN; Tefé 2M MNHN. **FRENCH GUIANA**: No locality data 1F BMNH. No locality data 1M BMNH; 1M MNHN.

Theope mundula Stichel, 1926

Figs. 29a-h; 97; 164; 229; 265.

Theope mundula Stichel, 1926. *Deut. ent. Zeit.* 1926: 96. **TL**: Monte Alegre, Río Pachitea, Peru. Holotype male ZMHU [Examined].

Identification and Taxonomy: Average forewing length: male 13mm, female 14mm.

MALE: *T. mundula* is distinguished from most "*sericea* group" species by having postdiscal brown androconial scaling on the DFW and it only closely resembles *T. barea*. *T. mundula* is a most variable species, even within a small geographical area, in its size (FW length 10-15mm), the shade of the ventral surface (pure pale yellow to more grainy, darker yellow), and the extent of the submarginal blue arc on the DFW (typically covers 4 vein spaces but ranges from 3-7), but the male genitalia, which are somewhat variable in the shape of the uncus, aedeagus and valvae, do not consistently differ between these phenotypes. The only character that can reliably be used to separate *T. mundula* from *T. barea* is the inwardly curving and increasingly smaller submarginal blue arc on the DFW that typically creates a smaller and darker area of postdiscal brown androconial scaling.

FEMALE: see the account of *T. barea* for a discussion of similar females (and below). It is possible that in the Amazon basin the females of *T. mundula* and *T. barea* are indistinguishable.

T. mundula has never been previously recognised to occur in Central America, but there are certainly two very similar but distinct "*sericea* group" phenotypes in that region, only one of which represents *T. barea*. The other I tentatively regard as being *T. mundula* because of the long blue dash in cell Cu1 and darker postdiscal brown scaling on the DFW of the male. In Central America, the two species are even more similar than they are in the Amazon basin. The male of *T. mundula* differs by the two aforementioned characters as well as by having blue only in the lower half of the discal cell of the DFW, and the female by having a rounded semicircle of blue instead of a triangle on the DFW. I considered describing the Transandean phenotype as a new subspecies, but since certain male Amazonian specimens have blue on the DFW that also does not extend beyond cell Cu1, although in that cell space it extends further distally, I refrain from doing so. Although there appear to be consistent differences in the females, the association of females with males in Amazon populations of "*sericea* group" species is currently so uncertain that I feel this is also not a compelling enough reason to recognise any subspecies at present.

Biology: Although this species is uncommon to rare in collections, in eastern Ecuador I have found males to be locally common perching in certain forested hilltop and ridgetop lightgaps. They perched beneath leaves 1 to 5 meters above the ground between about 1310 and 1515h, often sympatrically and synchronically with other "*sericea* group" species such as *T. lampropteryx*, *T. aureonitens*, *T. barea* and *T. dabrerai* (see Fig. 6c). The considerably rarer females are encountered in large forest lightgaps from mid-day to early afternoon.

Distribution: *T. mundula* is known to occur in disjointed localities in Central America, in the Guianas and along the length of the Amazon river. An outlying record from Espírito Santo state in south-east Brazil, if not mislabelled, suggests a broader southern Amazon distribution.

Specimens Examined: 57M 20F

HONDURAS: *Cortés*, La Cambre 4M, 1F BMNH; No locality data 1M BMNH. **PANAMA**: *Panamá*, Cerro Campana 1M, 1F USNM; *Canal Zone*, Gamboa 1M AME; Piña 1F FSCA. **ECUADOR**: *Napo,* Limoncocha (Feb) 1M USNM; Campo Anaconda, nr. Coca (Apr) 2M JHKW; Río Tiputini (Mar, Jul, Sept) 6M JHKW; Chichicorrumi (Feb, Oct, Dec) 4M, 1F JHKW; Finca San Carlo (Sept) 2M, 1F JHKW; Apuya (Jun, Oct) 3M JHKW; 1M RCB; No locality data 1M BMNH; 1F ZMHU. **PERU**: *Loreto*, Pebas 1M BMNH; Iquitos 2M, 1F MNHN; 1M AMNH; *San Martín*, Juanjuí 7M MNHN; Chazuta 1M MNHN; *Huánuco*, Monte Alegre, Río Pachitea 4M ZMHU; *Madre de Dios*, Parque Nacional del Manu, Pakitza 1M USNM; 30 km S.W. of Puerto Maldonado 1F DA. **BRAZIL**: *Amazonas*, São Paulo de Olivença 1M BMNH; Ipiranga 4M, 2F MNHN; *Pará*, Pará 1F BMNH; Amazons 2F BMNH; *Espírito Santo*, Linhares 1M AME. **FRENCH GUIANA**: *Cayenne*, Route de L'est 1M USNM; Kourou 1M JHKW; Mt. du Favard 1M JHKW; Mt. du Kaw 3M JHKW; *Saint Laurent du Maroni*, Saint Laurent du Maroni 1M MNHN; No locality data 6F BMNH. No locality data 1F MNHN.

Theope aureonitens Bates, 1868

Figs. 3a-c; 30a-d; 98; 165; 266.

Theope aureonitens Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 405. **TL**: Ega, W. Brazil. Syntype male and female BMNH [Examined]; Lectotype male BMNH [Designated].

Identification and Taxonomy: Average forewing length: both sexes 12.5mm.

MALE: the postdiscal area of pale brown androconial scaling on the DFW, which is significantly larger than that of *T. barea* and *T. mundula* and covers most of the distal portion of the wing, the pale blue dorsal coloration that is restricted to the discal cell and anal margin of the DFW and extends to the costal margin of the DHW, combined with a rich chrome yellow ventral surface and rounded wing shape are diagnostic for this species. The exact shade of the postdiscal brown scaling on the DFW is somewhat variable in *T. aureonitens* and noticeably darker in Guianan specimens. The male genitalia of *T. aureonitens* are most similar to those of *T. galionicus* and *T. dabrerai*, whose ventral surfaces are also chrome yellow, but the last sternite shape of each is most distinctive; the last tergite shape of *T. aureonitens* most closely resembles that of *T. galionicus*, and these taxa are probably sister species.

FEMALE: there is only a single specimen, a type, that purportedly represents the female of this species. Its rounded, compact wing shape and entirely pale brown dorsal surface are diagnostic.

Due to the slight uncertainty concerning the conspecificity of the male and female syntypes of *T. aureonitens*, I designate the male syntype as a lectotype. This specimen in the BMNH bears the following labels: "aureonitens", "Theope/aureonitens,/Bates./Godman-Salvin/Coll. 1914.-5.", "Ega,/U. Amazons./H.W. Bates.", "Type/H.T.".

Biology: In eastern Ecuador, males were found as solitary individuals in lightgaps along flat forest trails as early as 0930h, but small groups may be more commonly encountered perching in hilltop lightgaps within 3 meters of the ground during the afternoon between 1330 and 1500h. I found this species to be slightly more common during the dry season.

Distribution: *T. aureonitens* is known from widespread localities in the Amazon and Guianan regions but most specimens have originated from the western Amazon. Kaye (1921) and Barcant (1970) also report it from Trinidad. The following additional localities have been reported to me by K. Willmott (pers. comm.) from COLOMBIA: *Putumayo*, Orito (JLC); and by J.-Y. Gallard (pers. comm.) from BOLIVIA: *Cochabamba*, Villa Tunari.

Specimens Examined: 29M 1F

ECUADOR: *Napo,* Río Tiputini (Sept) 1M JHKW; Chichicorrumi (Dec) 1M JHKW; Finca San Carlo (Feb, Apr, Aug, Sept) 6M JHKW; Pimpilala (Feb) 3M JHKW; No locality data 2M BMNH. **PERU**: *Loreto*, Iquitos 2M MNHN; Balsapuerto 1M MNHN; Río Sucusari, Explornapo-Aceer 2M USNM; *San Martín*, Jepelacio 1M MNHN. **BRAZIL:** *Amazonas*, Tefé 1M, 1F BMNH; Manicoré 1M MNHN; Ipiranga 1M MNHN; 1M MCZ; Rio Umarí 2M MNHN. **FRENCH GUIANA**: *Cayenne*, Cayenne 1M BMNH; Route de L'est 2M USNM; No locality data 1M BMNH.

Theope galionicus Gallard & Brévignon, 1989

Figs. 31a-d; 99; 166; 230; 266.

Theope galionicus Gallard & Brévignon, 1989. *Bull. Soc. Sci. Nat.* 63: 5, figs. 15, 16. **TL**: Compté, French Guiana. Holotype male in coll. L. & C. Brévignon, Guadeloupe; type illustration [Examined].

Identification and Taxonomy: Average forewing length: male 13mm, female 14mm.

MALE: the chrome yellow ventral surface and semicircular pattern of blue on the DFW of *T. galionicus* mean that it can only be confused with *T. sericea* and *T. dabrerai*. It differs from *T. sericea* by having a more semicircular blue patch on the DFW whose distal margin has an angle of about 45° instead of about 75°, a more prominent black notch marking the discal cell end of the DHW, a broader and often more uneven distal black margin on the DHW, and, most notably, by having long androconial hairs at the anal margin of the VFW. Despite the remarkable wing pattern similarities, the male genitalia of the two species are quite different in the shape of the valvae and aedeagus, as are the last tergite and sternite. In these regards, *T. galionicus* is more similar to *T. dabrerai* but its last sternite is laterally compressed and partially bifurcate at the tip instead of rounded and its last tergite has a small projection from the lower posterior corner. *T. galionicus* also differs from *T. dabrerai* by having reduced blue along the anal margin of the DFW below vein 1A+2A, a broader black distal margin on the DHW and a broad black region at the costal margin of that wing (blue is variably present in cell Rs but never in cell Sc+R1) with a black notch at the discal cell end and, again most notably, by having long androconial hairs at the anal margin of the VFW. The similar male genitalia, last tergite and last sternite shapes indicate a close relationship to *T. aureonitens*.

FEMALE: the female of *T. galionicus* is reported as being unknown in the original description but two females in the BMNH, from French Guiana, very closely approximate the male of this species in dorsal wing pattern and one of these is illustrated here as the putative female. It is very similar to the female of *T. mundula* but has a vertical distal margin to the blue of the DFW instead of an inwardly diagonal one, and slightly more blue in the costal area of the DHW, with a distinctive black notch at the discal cell ends of that wing, as in the male.

Biology: No natural history information was provided by Gallard and Brévignon (1989) in the original description.

Distribution: *T. galionicus* is known from disparate localities in the Guianas and Amazon basin but has not yet been recorded from the base of the eastern Andes.

Specimens Examined: 11M 2F

PERU: *Loreto*, Iquitos 3M MNHN; San Roque, Iquitos 1M AME. **BRAZIL**: *Amazonas*, Ipiranga 4M MNHN; 1M MCZ. **FRENCH GUIANA**: *Cayenne*, Cayenne 1M BMNH; No locality data 1M, 2F BMNH.

Theope dabrerai Hall & Willmott, 1996

Figs. 32a-d; 100; 167; 266.

Theope dabrerae Hall & Willmott, 1996. *Trop. Lepid.* 7(1): 64-66, figs. 5a,b. **TL**: Finca San Carlo, km 12 Tena-Puyo rd., E. Ecuador. Holotype male to be deposited in the BMNH [Examined].

Identification and Taxonomy: Average forewing length 13.5mm.

MALE: *T. sericea* is similar to *T. dabrerai* in wing pattern but the male genitalia are quite different; while the morphology of *T. aureonitens* is more similar, it is readily distinguished on the basis of wing pattern characters. Overall, *T. dabrerai* is probably most similar to *T. galionicus* but it differs by having more extensive blue below vein 1A+2A at the anal margin of the DFW, blue in cell Sc+R1 at the costal margin of the DHW, and by lacking a black notch at the discal cell end of the DHW and long androconial hairs along the anal margin of the VFW. The last tergite of *T. dabrerai* is more elongate in its dorsal portion than that of *T. galionicus* and lacks a small projection from its lower posterior corner, and the last sternite is broader and more two dimensional, with a longer invaginated portion that connects to the genital armature and a rounded instead of bilobed tip; these structures of *T. dabrerai* are more similar to those of *T. sericea* and *T. lampropteryx*.

FEMALE: the putative female of *T. dabrerai* differs from that of *T. sericea* by having a slightly more compact wing shape, a more abrupt end to the blue of the discal cell of the

DFW, slightly less blue in the remaining forewing cells and an entirely blue discal cell on the DHW.

On a nomenclatural note, the name of this species was incorrectly formed in the original description with the feminine ending "-ae", and this is corrected here to the masculine ending "-ai".

Biology: Solitary males of this very rare species have been found perching 2 to 4 meters above the ground in forested hilltop lightgaps between 1400 and 1500h in the company of other *Theope* species. It has been found throughout the year in both wet and dry seasons.

Distribution: *T. dabrerai* is currently only known from eastern Ecuador but is assumed to have a broader west Amazonian distribution.

Specimens Examined: 5M, 1F

ECUADOR: *Sucumbíos*, Garzacocha, La Selva 1M PJD; *Napo,* Chichicorrumi (Jul, Dec) 2M JHKW; Jatun Sacha (Oct) 1M DA; 5 km S. of Puerto Napo (Sept) 1F DA; km 12 Tena-Puyo rd., Finca San Carlo (Feb) 1M JHKW.

Theope sericea Bates, 1868

Figs. 33a-d; 101; 168; 266.

Theope sericea Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 404. **TL**: Rio Tapajós, E. Brazil. Syntype male and female BMNH [Examined]; Lectotype male BMNH [Designated].

Identification and Taxonomy: Average forewing length: male 15mm, female 16mm.

MALE: *T. sericea* variably possesses a large round black spot in the discal cell of the DHW. If this is present it is diagnostic, but otherwise *T. sericea* may look very similar to *T. galionicus* and *T. dabrerai*. This phenotype differs from *T. galionicus* primarily by lacking long androconial hairs at the anal margin of the VFW and by having a larger blue area on the DFW that has a steeper angle to its distal margin, and from *T. dabrerai* by its larger size and darker blue dorsal coloration that does not extend to the costal margin of the DHW and is greater in extent on the DFW. The male genitalia of *T. sericea* are markedly different to those of both aforementioned species and has a dorso-ventrally elongate valve shape that parallels the vinculum with a posteriorly pointed semicircle at its apex, and a very short, broad and terminally pointed aedeagus that has numerous internal pencillate cornuti; the male genitalia of specimens with and without a black discal spot on the DHW do not differ.

FEMALE: the syntype female designated for *T. sericea* is in fact *T. excelsa* and another phenotype is illustrated here as the putative female. It can be distinguished from the females of *T. mundula* and *T. galionicus* by having a semicircular blue patch on the DFW that extends to the tornus. The greater extent of blue on the DFW and increased area of dark brown at the costa of the DHW separate it from female *T. dabrerai.*

Given the mixed type series for *T. sericea*, it is necessary to designate the male syntype as a lectotype to maintain stability. This specimen in the BMNH bears the following labels: "sericea", "Theope/sericea,/Bates./Godman-Salvin/Coll. 1914.-5.", "Tapajos,/Amazons./H.W. Bates.", "Type/H.T.".

Biology: Nothing is known about the biology of this rare species.

Distribution: *T. sericea* has a wide Amazonian range but the vast majority of specimens originate from the lower Amazon and Guianan regions, and it is only through recent intensive faunal survey work in Madre de Dios department of Peru by G. Lamas and colleagues that the species has been shown to occur in the western Amazon. The record of *T. sericea* from the upper Putumayo region of southern Colombia (Salazar, 1995) should be regarded as erroneous until it can be confirmed.

Specimens Examined: 11M 2F

PERU: *Madre de Dios*, Boca Río La Torre (Feb) 1M USNM; 20 km S.W. of Puerto Maldonado (Oct) 1M USNM. **BRAZIL**: *Pará*, Obidos 1M BMNH; Itaituba 1M ZMHU; Rio Tapajós 1M BMNH; Amazon 1M BMNH; *Maranhão*, No specific locality 1F BMNH; 1F ZMHU. **GUYANA**: *Cuyuni/Mazaruni*, Bartica 1M BMNH. **FRENCH GUIANA**: *Cayenne*, Cayenne 1M BMNH; No locality data 3M BMNH.

Theope lampropteryx Bates, 1868

Figs. 34a,b; 102; 169; 266.

Theope lampropteryx Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 404. **TL**: Santarem, E. Brazil. Syntype male BMNH [Examined].

Identification and Taxonomy: Average forewing length: male 16mm.

MALE: *T. lampropteryx* is quite distinctive and distinguished from other species with similarly brilliant chrome yellow ventral surfaces in the "*sericea* group" by its bright, dark blue dorsal coloration that covers the entire hindwing but only a small area at the base and along the anal margin of the forewing; it additionally differs from the most similar species *T. aureonitens*, by its larger size and lack of pale brown androconial scaling on the DFW. The extent of blue on the DFW in *T. lampropteryx* is geographically variable and while specimens from the base of the Andes have a solid blue bar along the anal margin of the DFW that extends almost to the tornus, those from the lower Amazon have this blue restricted to a more basal area; clinal intergrades exist between these two extremes. The male genitalia of the two aforementioned species are rather different and those of *T. lampropteryx* are most notable for the unique autapomorphy of possessing several rows of small spines along the ventral surface of the everted aedeagal vesica; its last tergite is also unusual in being dorsally split towards the tip.

FEMALE: unknown.

Biology: This species is very rare in institutional collections, but in eastern Ecuador, although this species is very local, in lowland primary forest sites below 600m, in particular ridgetop or hilltop lightgaps it can be quite common. In such a site in the undulating terrain of the upper Río Tiputini, males were found perching within 4 meters of the ground between 1330 and 1500h. As one individual was captured, another would appear to replace its perching place on the same leaf. Interestingly, the phenotypically similar *T. mundula* could be found perching on the same bush during the same period of the day, but it typically perched on a different clump of leaves. In Ecuador it appears to be present throughout much of the year.

Distribution: *T. lampropteryx* occurs in the Guianas and along the length of the Amazon from the base of the Andes to the Atlantic.

Specimens Examined: 24M

ECUADOR: *Napo,* Río Napo 1M BMNH; Río Tiputini (Mar, Sept) 4M JHKW; Jatun Sacha (Nov) 1M DA; Finca San Carlo (Apr, Sept) 3M JHKW; *Morona-Santiago,* Taisha (Jun) 1M JHKW; No locality data 4M BMNH. **PERU**: *Loreto*, Pebas 1M ZMHU; *San Martín*, Chazuta 1M MNHN. **BRAZIL:** *Amazonas*, São Paulo de Olivença 1M ZMHU; Ipiranga 3M MNHN; Rio Umarí 1M MNHN; *Pará,* Santarem 1M BMNH; Amazonas 1M ZMHU. **FRENCH GUIANA**: No locality data 1M BMNH.

GROUP VIII: Miscellaneous

Theope eurygonina Bates, 1868

Figs. 35a-d; 103; 170; 231; 267.

Theope eurygonina Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 410. **TL**: Santarem, E. Brazil. Syntype male and female BMNH [Examined].

= ***Theope eurygonina*** var. ***columbiana*** Staudinger, 1888. *Exot. Schmett.* 1: 263. **TL**: Río San Juan, W. Colombia. Syntype males and female ZMHU [Examined]. [**n. syn.**]

Identification and Taxonomy: Average forewing length: both sexes 15.5mm.

Sexes similar but female has more rounded wings and paler dorsal blue coloration that leaves an uneven brown border at the distal margin of the DHW. *T. eurygonina* is such a highly distinctive species, with no extant close relatives, that its exact phylogenetic position within the genus is uncertain, although morphological cladistic analyses place it as the most plesiomorphic species in *Theope* (Hall, in prep.). The species exhibits numerous autapomorphies, including three parallel brown bands on the ventral surface along with large, prominent submarginal ocelli, male genitalia that have markedly bifurcate valvae with a long lower projection and a large aedeagus with two scobinate patches at the tip of the everted vesica, and female genitalia that have a very long "boomerang"-shaped corpus bursae without signae and a very short but broad and heavily creased ductus bursae.

The male syntype of *T. eurygonina* is a rather worn and atypical specimen with a poorly contrasted ventral surface, unusually pointed wings and slightly reduced blue on the DFW. The wing pattern of the taxon *columbiana*, described from four males and a female from west Colombia, is actually more typical of specimens from east of the Andes and I therefore synonymise it with *T. eurygonina*.

Biology: This uncommon species occurs in intact wet forest habitats from sea-level to 1000m. In eastern Ecuador, I have found solitary males of *T. eurygonina* perching from 2 to 7 meters above the ground in large ridgetop and hilltop lightgaps, as well as clearings on any stepped slopes of these topographical features, between 1300 and 1515h. A single female was encountered flying low to the ground in one such ridgetop lightgap at 1315h.

Distribution: *T. eurygonina* occurs throughout the Guianan and Amazon regions and is also known from a disjunct locality in western Colombia, suggesting its presence in western Ecuador.

Specimens Examined: 37M 13F

COLOMBIA: *Chocó*, Río San Juan 3M BMNH; 4M, 1F ZMHU. **ECUADOR**: *Pastaza,* 8 km S. of Shell (Oct) 1M DA; 32 km S. of Puyo (Oct) 2M RCB; *Napo,* Yasuní 1F FSCA; Río Coca 1F AME; Río Tiputini (Mar) JHKW; Misahualli (Sept) 1F FSCA; Atahualpa (Sept) 1M JHKW; Puerto Napo (Oct) 1M GWB; km 4 Tena-Pano rd. (Sept) 1F DA; Finca San Carlo (Feb) 2M JHKW; Apuya (May, Oct) 1M, 1F JHKW; 1M RCB; *Morona-Santiago,* Taisha (Jun) 1M JHKW. **PERU**: *Loreto*, Iquitos 1F ZMHU; *San Martín*, Juanjuí 1M MNHN; *Puno*, Yahuarmayo 1M BMNH; *Madre de Dios*, Río La Torre 1F DA. **BRAZIL**: *Amazonas*, Maués 1M BMNH; *Pará*, Pará 1M ZMHU; Rio Tapajós 1M BMNH; Itaituba 1M, 1F ZMHU; Santarem 2M, 2F; 1M MNHN. **GUYANA**: No locality data 1M BMNH. **FRENCH GUIANA**: *Cayenne*, Galion 5M, 1F USNM; Route de L'est 2M USNM; *Saint Laurent du Maroni*, Saint Laurent du Maroni 1M AME. No locality data 1M, 1F BMNH; 1M MNHN.

Theope speciosa Godman & Salvin, 1897

Figs. 36a-d; 104; 171; 232; 267.

Theope speciosa Godman & Salvin, 1897. *Trans. ent. Soc. Lond.* 45(2): 245. **TL**: Río San Juan, W. Colombia. Holotype male ZMHU [Examined].

= ***Theope fasciata*** Lathy, 1904. *Trans. ent. Soc. Lond.* 52(3): 467, pl. 27, fig. 10. **TL**: Not stated. Holotype male BMNH [Examined].

= ***Theope phineus*** Schaus, 1913. *Ann. Mag. nat. Hist.* 8(11): 302. **TL**: Limón, Costa Rica. Syntype female USNM [Examined].

Identification and Taxonomy: Average forewing length: male 17.5mm, female 16mm.

MALE: the dorsal surface of *T. speciosa*, with its bright blue hindwing, and forewing with blue at the base and purple in the apex that tapers into faint scaling towards the tornus, is diagnostic. In fact, the wing pattern, male genitalia and last male abdominal tergite (which is the longest in the genus and split dorsally in the distal quarter) of *T. speciosa* are so unusual that it has no identifiable sister species. A consilience of morphological characters, however, including certain female genitalic characters such as a semi-sclerotised ductus seminalis, places *T. speciosa* nearest the "*pedias* group". It superficially resembles certain species of the "*virgilius* group", where Godman and Salvin (1897) placed it, but the tornal spots of the VHW are smaller and have white instead of bluish white shading proximally.

FEMALE: the dorsal surface of female *T. speciosa* does somewhat resemble that of *T. pedias* and relatives, to which it appears to be most closely related, as well as that of many "*theritas* group" species, but the variably present arcing blue in the tornus of the DFW and tornal spots of the VHW readily distinguish it from them. Female *T. speciosa* overall most closely approximates certain "*foliorum* group" species, such as the partially sympatric *T. lycaenina* and *T. wallacei*, but these species do not have such an obvious postdiscal extension to the blue of the DFW, and on the ventral surface they have evenly sized black spots around the entire hindwing and often forewing submargins, without any prominent proximal white scaling.

The taxon *fasciata* was correctly recognised as a synonym of *T. speciosa* by Stichel (1911) as was the taxon *phineus*, described from a female, by DeVries (1997).

Biology: *T. speciosa* is a rare inhabitant of lowland rainforests. In north-west Ecuador, two females were found flying 2 to 3 meters above the ground at the edge of a hilltop lightgap between 1230 and 1330h. No males were encountered here and in fact there are no perching data available for them, unusally the rarer of the two sexes.

Distribution: *T. speciosa* is known to range from Costa Rica to north-west Ecuador. The following additional localities have been reported to me by K. Willmott (pers. comm.) from COLOMBIA: *Valle de Cauca*, Río Tatabro (JS).

Specimens Examined: 7M 24F

COSTA RICA: *Limón*, Cahuita 1F USNM; Limón 1F USNM. **PANAMA**: *Bocas del Toro*, No specific locality 1F USNM; *Panamá*, El Llano 1F USNM; *Canal Zone*, Piña 1M, 9F AME; 1F FSCA; 2F USNM; Gatun 1M, 3F USNM; Barro Colorado Is. 1M MCZ; *San Blas*, Río Armila 1F USNM; No locality data 1M FSCA. **COLOMBIA**: *Chocó*, Río San Juan 1M, 1F ZMHU; *Cauca*, Río Micay 1M MNHN. **ECUADOR**: *Esmeraldas,* km 17 San Lorenzo-Ibarra rd. (Dec) 2F JHKW. No locality data 1M, 1F BMNH.

Theope pieridoides C. & R. Felder, 1865

Figs. 37a-d; 105; 172; 233; 267.

Theope pieridoides C. & R. Felder, 1865. *Reise Novara* 2: 292, pl. 37, figs. 19, 20. **TL:** Bahia, E. Brazil. Syntype female BMNH [Examined].

= ***Theope bahlmanni*** Fassl, 1922. *Ent. Zeit.* 36(12): 46. **TL:** Santarem, E. Brazil. Syntype male unknown. **[n. syn.]**

Identification and Taxonomy: Average forewing length: both sexes 17mm.

Sexes similar but female has slightly more rounded wings. *T. pieridoides* is instantly recognisable and unique within the genus in possessing a pure white ventral surface and a largely white dorsal surface with only the forewing apices black. The male genitalia are equally unusual in the shape of the uncus, valvae and aedeagus, as is the shape of the last abdominal tergite and sternite, which has unique short and angular lateral projections. The nearest relative of this species is somewhat uncertain, but a consilience of characters used in a cladistic analysis (see introductory "Taxonomy" section) currently places it near *T. cratylus*. *T. pieridoides* is quite variable in size and the extent of black in the apex of the DFW.

Anton Fassl was an ardent professional collector of Lepidoptera at the beginning of the Twentieth Century but very rarely did he describe his own material. The original description of his taxon *bahlmanni* reads exactly like a description of *T. pieridoides* and certainly gives no indication that it is a taxonomic entity distinct from that species. Thus, although no type specimen is known, I formalise the suspicions of Stichel (1930) in synonymising *bahlmanni* with *T. pieridoides*.

Biology: I have never seen *T. pieridoides* in nature but judging by its museum locality data, which shows the species to circumvent the Amazon basin, it seems likely that it predominantly inhabits drier forest types. Watson and Whalley (1975) state that in Bahia, eastern Brazil, *T. pieridoides* flies with a white pierid-like hesperiid in the genus *Leucochitonea* Wallengren, 1857, with which they suggest it may be involved in mimicry.

Given the extraordinary phenotypic divergence of *T. pieridoides* from the typical *Theope* baüplan, it is tempting to look to mimicry for the explanation but proof is decidedly lacking. The pure white ventral wing surface may instead be an adaptation to enhanced camouflage in drier habitats. Barcant (1970) reports consistently finding *T. pieridoides* in Trinidad, on the outer foliage of a particular tree over a period of ten years, suggesting either that the species is sedentary around its foodplant or, more likely, that the males maintain specific perching sites.

Distribution: *T. pieridoides* occurs from Mexico to western Ecuador, through Colombia and northern Venezuela, on the island of Trinidad, and around the eastern rim of the Guianas and Brazil as far south as Rio de Janeiro and up the Amazon as far as west as Santarem. The following additional localities have been reported to me by K. Willmott (pers. comm.) from COLOMBIA: *Meta*, Cubarral (JS) and ECUADOR: *El Oro,* Uzchcurrumi (QCAZ); and are listed by Brown and Mielke (1967) for BRAZIL: *Espírito Santo*, Leopoldina.

Specimens Examined: 31M 21F

MEXICO: No locality data 1F BMNH. **HONDURAS**: *Cortés*, La Cambre 2M BMNH. **VENEZUELA**: *Carabobo*, Las Quiguas 1M BMNH; Puerto Cabello 1F ZMHU. **COLOMBIA**: *Cundinamarca*, La Mesa 1F BMNH. **ECUADOR**: *Bolívar,* La Chima, Rio de las Juntas 2M, 1F BMNH. **BRAZIL**: *Pará*, Santarem 1M BMNH; Rio Xingu 1F MNHN; Pará 1F BMNH; *Pernambuco*, Tiúma 2F USNM; *Bahia*, No specific locality 1M, 4F BMNH; 1M ZMHU; *Mato Grosso*, Cuiabá 1F BMNH; *Minas Gerais*, Mariana 1M BMNH; No specific locality 1M BMNH; *Rio de Janeiro*, Rio de Janeiro 2M BMNH; No locality data 1M BMNH. **FRENCH GUIANA**: *Cayenne*, Cayenne 1F BMNH; No locality data 3M BMNH. **TRINIDAD**: Port of Spain 1M ZMHU; San Fernando Hill 1M

BMNH; Hololo 1M, 1F AME; Tunapuna 1F AME; St. Annes 1M MNHN; No locality data BMNH; 1F AME; 1F USNM; 6M AMNH. No locality data 2M, 3F BMNH; 3M ZMHU.

Theope cratylus Godman & Salvin, 1886

Figs. 38a-d; 106; 173; 234; 267.

Theope cratylus Godman & Salvin, 1886. *Biol. centr.-amer., Lep. Rhop.* 1: 484; 3: pl. 46, fig. 9. **TL**: David, Panama. Holotype male BMNH [Examined].

Identification and Taxonomy: Average forewing length: both sexes 19mm.

Sexes similar but female slightly larger with more rounded wings and paler dorsal blue coloration that extends slightly further towards the distal margin on the forewing and has more exaggeratedly concave elements to its distal margin. *T. cratylus* has a more pointed wing shape than *T. virgilius*, often a paler ventral surface, small black spots in the tornus of the VHW that have no blue or white proximal scaling and an apically directed pointed triangle of blue on the DFW that has concave elements to its distal margin. In many of these respects, *T. cratylus* is similar to *T. villai*, but *T. cratylus* has dark brown scaling at the base of cell Cu2 on the VFW and lacks the white spots at the apex of the blue triangle on the DFW that in *T. villai* extends further towards the anal margin, the angular hindwing shape and the cell end markings and darker submarginal shading of the VHW. *T. cratylus* is also larger than both of these species and has most distinctive male genitalia that are made up of a peculiar mixture of characters; these include a unique long square-tipped aedeagus, valvae like those of "*theritas* group" species, and a strongly bifurcate last abdominal sternite that it shares only with the two members of the "*antanitis* group". A consilience of characters places *T. cratylus* closest to this last species group.

Biology: Very little is known about the biology of this uncommon species. De la Maza and de la Maza (1993) state that in Chiapas, Mexico, it occurs from sea-level to 900m in hot and semi humid forest and DeVries (1997) reports that G. B. Small found it during the dry season and early rainy season in the Canal Zone of Panama. From the locality data listed below it is evidently at least tolerant of drier forest habitats, and it is the only *Theope* species, along with *T. publius incompositus*, known to inhabit the very dry Yucatán Peninsula of Mexico; no *Theope* species are listed by de la Maza & Bezaury (1992) for Quintana Roo state in that peninsular.

Distribution: *T. cratylus* occurs from southern Mexico to north-west Colombia. De la Maza and de la Maza (1993) give details on its occurrence in southern Chiapas state, Mexico, citing the regions of Cuenca del Grijalva, Soconusco and Sierra Madre. The following additional localities are listed by Meerman (1999) for BELIZE: *Corozal*, No specific locality; by Austin *et al.* (1996) for GUATEMALA: *El Petén*, Tikal; and by DeVries (1997) for COSTA RICA: *Alajuela*, Río Virilla de Guacima; *Heredia*, Chilamate; *Limón*, Germania.

Specimens Examined: 20M 23F

MEXICO: *Guerrero*, Acahuizotla 1M, 2F AME; Mexcala 1M AME; *Oaxaca*, Rancho San Carlos 1M AMNH; *Veracruz*, Catemaco 2F AME; Soteapán 2M AME; *Quintana Roo*, E. of X-can 1F FSCA; *Chiapas*, Pichucalco 1M AME; Santa Rosa, Comitán 1M AME. **HONDURAS**: *Cortés*, La Cambre 1M BMNH. **COSTA RICA**: *San José*, Colon (600m) 1F USNM; *Alajuela*, San Mateo 1M USNM; *Limón*, Guapiles 1F USNM. **PANAMA**: *Chiriquí*, David 1M BMNH; Bugaba 1M USNM; No specific locality 1F BMNH; 1F ZMHU; 1M, 1F MNHN; *Panamá*, Cerro Campana (1000ft) 1M, 1F AME; *Canal Zone*, Cocoli 1M, 1F AME; 1M USNM; Piña 1F FSCA; Farfan 1F AME; La Pita

1M, 1F USNM; Ft. Clayton 1F USNM; Paraiso 1M, 4F USNM; Madden Forest 1M, 1F USNM; Gatun 1F DA; *Veraguas*, No specific locality 1M MNHN. **COLOMBIA**: *El Cesar*, Lake Zapatosa, Chiriguaná 1M BMNH. No locality data 1F AMNH.

GROUP IX: "*antanitis* group"

Theope sisemina Seitz, 1920

Theope sisemina sisemina Seitz, 1920

Figs. 39a-h; 107a; 174a; 235; 267.

Theope eurygonina f. ***sisemina*** Seitz, 1920. In: *Seitz Grossschmett. Erde* 5: 726. **TL**: Río Dagua, W. Colombia. Holotype unknown; type illustration [Examined].

Identification and Taxonomy: Average forewing length: male 16mm, female 17mm.

Sexes similar but female has a more rounded wing shape. Although superficially similar to *T. eurygonina*, *T. sisemina* is morphologically very different and unequivocably the sister species of *T. antanitis*. *T. sisemina* is a smaller species with blue at the base of both dorsal wing surfaces, markedly reduced white on both wing surfaces, a predominantly brown ventral surface and more prominent submarginal spots on the VHW. The male genitalia of the two species do not differ significantly. *T. sisemina sisemina* is a most variable taxon in the size and width of the dorsal postdiscal white band (and thus that of the ventral surface), which may be as broad as the basal blue region or very thin and almost absent, especially on the hindwing. Some of this variation can be ascribed to geographic location (i.e. different valleys), but the influence of altitude, the extent of intrapopulation variation and the reoccurrence of particular phenotypes in disparate localities render the recognition of further subspecies inadvisable.

Incredibly, despite significant phenotypic and ecological differences, *T. sisemina* was described as a form of *T. eurygonina* and was not raised to specific rank until a rarely unambiguous taxonomic statement to this effect was made by D'Abrera (1994). The sex of the holotype, whose whereabouts is not known, is not stated in the original description (Seitz, 1920).

Biology: *T. sisemina* and, almost certainly, its sister species *T. antanitis*, are the only *Theope* species to exclusively occur in cloud forest habitats. In Ecuador, I have encountered *T. sisemina sisemina* between 1550 and 2000m, although it may have a slightly broader altitudinal range than this. The majority of known specimens originate from the environs of Baeza, and here two males were found perching atop a small bush only 2 meters high at 1300h, at the edge of a mountain pasture, fairly distant from good forest habitat but close to some remnant riverine vegetation. In contrast, near La Bonita, a male was found perching high (6-8 meters) up in a forested hillside lightgap with other species of riodinids and lycaenids at about 1400h. Individuals have been collected during the sunniest months of the year in east Ecuadorian cloud forest habitats, from September to March..

Distribution: This subspecies is only known from west Colombia and east Ecuador but it surely occurs on both slopes of the Andes in these countries.

Specimens Examined: 12M 2F

COLOMBIA: *Risaralda*, nr. Pueblo Rico 1F JS. **ECUADOR**: *Zamora-Chinchipe,* km 40/55 Loja-Zamora rd. (Feb, Dec) 2M SA; *Morona-Santiago*, Río Abanico (Nov) 1M DT; *Tungurahua,* Río Verde (5000ft) 1M BMNH; *Napo,* Baeza (Sept, Oct, Nov) 3M JHKW; 1M, 1F USNM; 2M RCB; 1M DA; *Sucumbíos,* km 9 La Bonita-Rosa Florida rd. (Mar) 1M JHKW.

Theope sisemina tabacona Hall & Willmott, 1996

Figs. 39i,j; 107b; 174b; 267.

Theope sisemina tabacona Hall & Willmott, 1996. *Trop. Lepid.* 7(1): 64-65, figs. 4a,b. **TL**: Río Tabaconas, N. Peru. Holotype male BMNH [Examined].

Identification and Taxonomy: Forewing length: male 16mm.

MALE: the subspecies *T. s. tabacona* has paler blue on the dorsal surface that covers the entire hindwing and forms a triangle at the base of the forewing with only a faint trace of white bisecting its apex; the ventral surface is paler and less contrasted with a much thinner postdiscal white band and evenly sized submarginal spots on the hindwing. This subspecies somewhat resembles *T. eurygonina* but is easily distinguished from it by lacking the three parallel brown ventral bands; the male genitalia of the two species are utterly distinct.

FEMALE: unknown.

Biology: The biology of this taxon is undoubtedly the same as that of the nominate.

Distribution: This subspecies is only known from the unique holotype from north Peru.

Specimens Examined: 1M

PERU: *Cajamarca*, Río Tabaconas (6000ft) 1M BMNH.

Theope antanitis (Hewitson, 1874) **[n. comb.]**

Figs. 40a,b; 108; 175; 267.

Lemonias antanitis Hewitson, 1874. *Desc. new spec. butts. Buckley Bolivia*: 15. **TL**: Bolivia. Syntype male BMNH [Examined].

Identification and Taxonomy: Forewing length: male 18mm.

MALE: this taxon has variably been treated in the genera *Lemonias*, *Polystichtis* and *Calospila*, the first two of these being used in the past to include species now placed in the latter. Its true systematic position has been a mystery ever since its description, and even its author, Hewitson (1874), stated it to be "very unlike any known species". Seitz (1920) believed it to be a species of *Pandemos* Hübner, [1819]. However, dissection of the syntype reveals it to be the sister species of *T. sisemina* and I therefore transfer *antanitis* to *Theope*. In fact, the male genitalia of the two species do not differ in any significant regard. *T. antanitis* is larger than *T. sisemina*, has only traces of blue-gray at the base of both dorsal wing surfaces, an entirely white DHW, more extensive white on the DFW that extends to the costa, a broader white postdiscal band and better defined discal brown band on both ventral wing surfaces, and less prominent ventral submarginal spots, especially on the hindwing.

FEMALE: unknown.

Biology: Nothing is known about the biology of this very rare species.

Distribution: *Theope antanitis* is currently only known from the unique syntype labelled "Bolivia". Its sister species relationship to *T. sisemina* suggests that it is very probably a cloud forest inhabitant and the syntype probably originates from the relatively well collected Yungas region of north-west Bolivia. The species undoubtedly also occurs in southern Peru and possibly further north in the Andes.

Specimens Examined: 1M

BOLIVIA: No locality data 1M BMNH.

GROUP X: "*virgilius* group"

Theope iani Willmott & Hall, 1994

Figs. 41a-f; 109; 176; 236; 268.

Theope iani Willmott & Hall, 1994. *Trop. Lepid.* 5(2): 88-89, figs. 4a-c. **TL**: La Punta, km 44 Lita-San Lorenzo rd., W. Ecuador. Holotype male and allotype female to be deposited in the BMNH [Examined].

Identification and Taxonomy: Average forewing length: male 16mm, female 17mm.

Sexes similar but female has a slightly more elongate wing shape with a more convex distal forewing margin and paler, brighter blue dorsal coloration that extends slightly further towards the forewing tornus. *T. iani* is superficially somewhat similar to *T. zostera* on the ventral surface but this species has more strongly contrasted, paler marginal elements, yellow markings surrounding the discal cell ends and no hindwing tornal spots. Although the wing shape of *T. iani* is most similar to that of "*theritas* group" species, several male genitalic and abdominal characters, including, most conspicuously, the highly modified "horn"-shaped last sternite, and the presence of bluish scaling proximal to the tornal spots of the VHW unequivocably place it in the "*virgilius* group". Cladistic analyses (see introductory "Taxonomy" section) indicate that it is the most plesiomorphic species of the group; it is readily distinguished from other members of the group by its wing shape and ventral pattern.

Specimens of *T. iani* from central Colombia have less contrasted, more uniformly brown ventral surfaces with more strongly marked discal cell ends. They may represent a distinct subspecies but more material from intervening areas is needed to assess this question.

Biology: Until recently, the only known material of this species consisted of two males in the BMNH collected by Rosenberg in 1897 during the first major lepidopteran expeditions to the north-west of Ecuador. It is rare and local in north-west and central-west Ecuador, occurring there from 300-900m, although a Colombian specimen reportedly originates from as high as 1500m (J. LeCrom, pers. comm.). I have encountered males only in a single forested ridgetop lightgap, where a small group were perching under large *Cecropia* leaves about 4 to 5 meters above the ground during the afternoon from 1245 to 1430h. A female was also found in the vicinity of this perching area and another was captured flying down the middle of a small river in the late afternoon. Since specimens have been captured in March, and from June to August, which encompass both dry and wet months, *T. iani* probably flies throughout the year.

Distribution: This species is currently known from western Ecuador and the valleys of central Colombia but it also undoubtedly occurs in the Chocó region of west Colombia.

Specimens Examined: 8M 4F

COLOMBIA: *Caldas,* Río Cauca 1F JS; Plan Alto (Mar) 1M JHKW; Marquetalia 1F JLC. **ECUADOR**: *Esmeraldas,* San Lorenzo-Ibarra rd., La Punta (Mar, Jun, Jul) 5M, 1F JHKW. *Imbabura,* Paramba (Mar) 2M BMNH; *Pichincha,* Río Tanti (Aug) 1F JHKW.

Theope villai Beutelspacher, 1981

Figs. 42a,b; 177; 237; 268.

Theope villai Beutelspacher, 1981. *An. Inst. Biol. Univ. Nal. Autón. de Méx., Ser. Zool.* (1): 395-398, figs. 1, 2. **TL**: Acahuizotla, Mexico. Holotype male UNAM; type illustration [Examined].

Identification and Taxonomy: Forewing length: male 16mm, female 17mm.

Sexes similar but female has a small subapical lilac blue patch on the DFW. Only the holotype male is referred to in the original description and the female is figured here for the first time; a male is illustrated in color by de la Maza (1987). *T. villai* is distinguished from the similar *T. virgilius* and *T. cratylus*, with which it occurs sympatrically in Mexico, by its more pointed and slightly angular hindwing shape, more yellow-ochre ventral ground color, which has darker discal cell end markings, and paler lilac blue dorsal coloration that on the forewing is more triangular and has white coloration in cells Cu1 and M3.

As far as can be told from the rather crude illustration in Beutelspacher (1981), the male genitalia of *T. villai* very closely resemble those of *T. virgilius* and *T. eupolis*, although the lower posterior corner of the uncus is markedly more produced and pointed. As illustrated in Beutelspacher (1981) (and reproduced in Fig. 177), the eighth male abdominal tergite is unique in the genus in possessing two prominent, outwardly curving projections from the lower posterior corner. The signae of the female genitalia are slightly shorter at the corpus wall than those of *T. virgilius* and *T. eupolis* and the ostium bursae is larger and broader.

Biology: This is a very poorly known species and only a single female specimen was located outside of Mexican collections. It is not even listed in the riodinid species-group catalogues of Bridges (1988, 1994). No ecological information was given in the original description, but de la Maza (1987) states that it occurs in semi-evergreen and deciduous seasonal forest, and the adults are known to fly in July and from November to January (Beutelspacher, 1981; de la Maza, 1987). Its restricted range and threatened habitat suggest that its conservation status should be "Vulnerable" (see introductory "Ecology" section).

Distribution: *T. villai* is known only from a small area of western Mexico, in Guerrero and Mexico states, where the species forms part of a sizeable endemic butterfly fauna (Luis *et al.*, 1991; Vargas *et al.*, 1991, 1996; Llorente and Escalante, 1992; Warren and González-Cota, 1996, 1998; Warren *et al.*, 1998), termed the "Teotepec-Loxicha" center of endemism by de la Maza (1987). The record by Balcázar (1993) of "*T.* aff. *villai*" from Pedernales in Michoacán state, Mexico, probably represents *T. virgilius*, which is not given in his checklist, but if true it would represent a relatively large range extension for this west Mexican endemic and it thus needs confirming. The following additional locality is given by de la Maza (1987) for MEXICO: *México*, San Nicolás Tolentino.

Specimens Examined: 1F

MEXICO: *Guerrero*, Acahuizotla (Jul) 1F AME.

Theope virgilius (Fabricius, 1793)

Figs. 43a-f; 110; 178; 238; 268.

Hesperia virgilius Fabricius, 1793. *Ent. Syst.* 3(1): 323; *Jones's Icones* pl. 37, fig. 3. **TL**: "Habitat in Indiis" [sic]. Types unknown; type illustrations [Examined].

= ***Theope caerulea*** Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 408. **TL**: South Brazil. Syntype female BMNH [Examined]. **[n. syn.]**

= ***Theope polimela*** Godman & Salvin, 1897. *Trans. ent. Soc. Lond.* 45(2): 247. **TL**: Cauca Valley (2500ft), Colombia. Syntype male BMNH and syntype male ZMHU [Examined]. **[n. syn.]**

Identification and Taxonomy: Average forewing length: male 18mm, female 17mm.

Although no extant type specimens are known for *T. virgilius*, the original type illustrations represent well the popular concept of that species and an ovoid black spot near the base of each forewing must be attributed to either damage on the specimen in question or artistic licence. I therefore deem a neotype designation unnecessary, especially in light of the fact that the types may reside unrecognised in the Macleay collection in Sydney, Australia (G. Lamas, pers. comm.) (see the account of *T. archimedes* for details).

MALE: the variable *T. virgilius* is easily confused with the equally variable *T. eupolis* and sometimes their spheres of variability come so close that certain specimens can be difficult to identify; the two species differ little on the ventral surface but on the dorsal surface, *T. virgilius* typically has more extensive blue on the forewing that often covers half the wing area and a completely blue hindwing that lacks the large black area at the center of the distal margin. The male genitalia of *T. virgilius* are also rather variable and some specimens have small external spines on the aedeagus, a character not seen elsewhere in the genus; the male genitalia along with the eighth abdominal tergite and sternite are not otherwise significantly different from those of *T. eupolis*.

FEMALE: females can be more difficult to separate from *T. eupolis* than males but as well as the distinguishing characters given above, female *T. virgilius* typically has pale blue instead of pale purplish blue dorsal coloration and a subapical blue patch on the DFW. The ostium bursae of the female genitalia is also broader in *T. virgilius*, and forms a more pronounced "U"-shape.

Two taxa, *caerulea* and *polimela*, were described as distinct species and subsequently placed as subspecies of *T. virgilius* by Stichel (1910). The first, *caerulea*, was described from a single female specimen seemingly on the grounds that its capture locality was very distant from the range of *T. virgilius*, which was thought to be exclusively Central America at that time; I find it to be a typical *T. virgilius* female and synonymise it with that species. The second, *polimela*, was described from two males that supposedly had more blue at the anal margin of the DFW than *T. virgilius*; again, these specimens fall within the normal range of variation for *T. virgilius* and I also synonymise *polimela* with it.

Biology: *T. virgilius* is one of the most common and widely known *Theope* species. It is somewhat of a habitat generalist, occurring in secondary growth habitats, forest edge and primary wet and semi-deciduous forest habitats from sea-level up to approximately 1300m. On one occasion, I even found females nectaring from *Lantana* flowers growing along the roadside in the middle of a built-up town. In the dry forest of south-west Ecuador, I found both sexes in association with thorny *Acacia* trees from mid-morning onwards. Interestingly, the ventral ground color of these specimens is atypically pale, indicating that perhaps the variation observed in ventral ground color is tied to habitat type and is an adaptation towards enhanced camouflage when the butterfly is at rest, in this case to a dry and sunny habitat of pastel colors. In the wet rainforest habitats of eastern Ecuador, I encountered males perching in hilltop and ridgetop lightgaps about 5 meters above the ground, in the late afternoon only between 1500 and 1630h. In Villavicencio, east Colombia, Callaghan (1983) found *T. virgilius* males hilltopping from 1140 to 1515h. Male perching behavior clearly varies intraspecifically and geographically and it is probably dependant on local climate, microhabitat and, perhaps above all, the number of microsympatric congeners. Once, a male was attracted to a fish-baited canopy trap deep in primary forest, a phenomenon that is most unusual for a member of the Nymphidiini (see introductory "Ecology" section). Both sexes are reported to feed on the flowers of *Casearia*, *Terminalia*, *Psychotria*, *Cordia*, *Pentaclethra*, *Inga* and certain herbaceous Asteraceae by DeVries (1997).

T. virgilius has been reared on several plants in two different families: unidentified *Inga* and *Swartzia* species in the Leguminosae and *Omphalea diandra* in the Euphorbiaceae (Mallet in Harvey, 1987; DeVries *et al.*, 1994; DeVries, 1997). The white egg of *virgilius*, which is always laid singly on growing shoots and leaves in the presence of *Azteca* ants (Dolichoderinae), is dorso-ventrally flattened and covered with a raised mesh of hexagons that extend to the very edge of the large dorsal micropylar area whose pores are situated around its circumference. The mature larva has a shiny black head capsule with a central inverted "V", a dense corona of prominent dark purple and black balloon setae on the prothoracic shield, a pale green body with a thin dark dorsal midline, a scattering of fine white spots on the dorsum and short white ventro-lateral setae, and a conspicuous whitish anal plate of a horny texture that is trimmed with black and has a brown medial portion. When not feeding, the solitary caterpillars hide in curled leaves that are fixed with silk; they eventually pupate here into simple, uniformly brown, cylindrical pupae (DeVries, 1997). DeVries (1997) should be consulted for an SEM of the eggs and a black and white drawing of the mature larva.

Distribution: This is one of the most widespread *Theope* species and it occurs throughout most of tropical Mexico and Central and South America, including numerous offshore islands. Most specimens in collections originate from Central America where it appears to be rather abundant but east of the Andes it is really quite rare. The following additional localities are listed by Warren *et al.* (1998 - *Co*), Vargas *et al.* (1996 - *Ja*) and Raguso & Llorente (1992 - *Ve*) for MEXICO: *Colima*, Platanarillos; *Jalisco*, Mismaloya, Río Tomatlán (Hwy 200); *Veracruz*, Laguna Encantada; by Meerman (1999) for BELIZE: *Belize*, No specific locality; *Cayo*, No specific locality; by Austin *et al.* (1996) for GUATEMALA: *El Petén*, Tikal; by DeVries (1997) for COSTA RICA: *Heredia*, Chilamate; *Limón*, Cahuita; *Puntarenas*, Isla del Caño, Sirena; and are reported to me by C. Jiggins (pers. comm.) from ECUADOR: *Loja*, Tambo Negro; and by J.-Y. Gallard (pers. comm.) from BOLIVIA: *Cochabamba*, Villa Tunari.

Specimens Examined: 294M 231F

MEXICO: *Tamaulipas*, 3 mi. N.W. of Gomez Farias 1M, 1F AME; *San Luis Potosí*, El Salto Falls 2M, 2F FSCA; 1M AME; Laurel Canyon, Axtla Juntia 1F USNM; Arroyo Seco 1F USNM; Tamazunchale 1F AMNH; No specific locality 1M AMNH; *Jalisco*, Chamela Bay 2F AMNH; *Colima*, Colima 1M, 2F BMNH; Comala 1M AME; *Morelos*, Huajintlan 2F AME; *Guerrero*, Acahuizotla 1F AME; Iguala 1F AME; No specific locality 3M, 1F BMNH; *Veracruz*, Veracruz 1F FSCA; Orizaba 1M USNM; 10 km S. of Veracruz 1M AMNH; Córdoba 1M BMNH; 1M AMNH; Antón Lizardo 1F FSCA; Presidio 4M, 2F AME; 4M, 4F AMNH; Catemaco 1M AME; 2 mi. W. of Nonchital 2F AME; Paso de San Juan 1M USNM; Rinconada 1F USNM; Jalapa 1F BMNH; Soteapán 2F AME; *Oaxaca*, 3 mi. S.E. of Tapanatepec 2F AME; Tuxtepec 2M AMNH; *Chiapas*, Tuxtla Gutierrez 1M, 2F FSCA; 16 mi. S.W. of Cintalapa 1F FSCA; No locality data 1M, 1F MNHN; 1F USNM. **BELIZE**: *Corozal*, Corozal 1M BMNH; *Toledo*, Punta Gorda 1M BMNH; Colombia 1M AMNH; ? Hummingbird Highway 1F FSCA; 1M, 1F AME. **GUATEMALA**: *Baja Verapaz*, San Jerónimo 6M BMNH; *Izabal*, Puerto Barrios 1M, 1F; *Santa Rosa*, Guazacapán 1M, 1F BMNH; Barberena 1M, 1F BMNH. **EL SALVADOR**: *San Salvador*, Sta. Tecla 1M, 2F AME; 2M USNM; Cerro San Jacinto, San Salvador 1M, 1F AME; Lago de Ilopango 1F AME; *La Libertad*, Tamanique (1000m) 1F AME; Los Chorros 1F AME; *La Paz*, San Esteban Catarina 2M, 1F AME; Los Planes 1M AME; *Cuscatlán*, Rosario 4M USNM. **HONDURAS**: *Cortés*, San Pedro Sula 3F BMNH; 1F USNM; La Cambre 1M BMNH; *Atlántida*, 18 km W. of La Ceiba 1F USNM; No locality data 6M, 7F BMNH; 1F USNM. **NICARAGUA**: *Atlántico Sur*, Rama 1F AME; Bluefields 2F AME; *Chontales*, No specific locality 2M, 3F BMNH. **COSTA RICA**: *Guanacaste*, La Cruz 1M FSCA; Cañas 1F FSCA; *Alajuela*, San Mateo 2M BMNH; Miravalles 1M BMNH; *Limón*, Cahuita 1M USNM; *Puntarenas*, Palmar

Norte 1M FSCA; No locality data 1M, 2F BMNH; 1M MNHN. **PANAMA**: *Chiriquí,* Bugaba 2M, 4F BMNH; 2M ZMHU; 2M, 1F USNM; Lino 1F MNHN; Río Tolé 1M, 1F USNM; No specific locality 1M, 2F BMNH; 3M, 3F ZMHU; 5M, 4F MNHN; *Veraguas*, Calobre 1M, 1F BMNH; No specific locality 1M BMNH; *Herrera*, Cerro Montinosa 1F USNM; *Coclé*, Río Hato 1F FSCA; *Panamá*, Cerro Campana (1000ft) 1M FSCA; Río Trinidad 1M USNM; Diablo Heights 2M USNM; Río Caimito, nr. La Chorerra 1M USNM; 5 km N. of El Llano 1M, 3F USNM; Archipiélago de las Perlas: Isla de Puercos 2F, Isal de Contadora 1M AMNH; *Colón*, Sta. Rita 1F USNM; Portobelo trail, Continental divide 1F AMNH; 4F AME; *Canal Zone*, Cólon 1M, 1F BMNH; Piña 1F FSCA; 1M AME; Pedro Miguel 1F BMNH; Gatun 2M AME; Balboa !M AME; Albrook Airbase 1M AME; 1F USNM; Lion Hill 2F BMNH; La Pita 1F USNM; Curundu 1M USNM; 1M AME; Matachin 1M BMNH; 1M AME; 2F USNM; Los Rios 2M, 3F USNM; Madden Forest 1M, 1F USNM; Cocoli 1M USNM; Farfan 4M, 1F USNM; Ft. Sherman 1F USNM; Barro Colorado Is. 1M, 1F AMNH; Empire 2M AMNH; La Boca 5M, 2F AMNH; end of locks 1M AMNH; Coco Solo 1M AMNH; Gamboa 1F AME; No specific locality 1F FSCA; 1M USNM; *San Blas*, Río Armila 2M, 2F USNM; *Darién*, Caña 1M, 1F ZMHU; 2F USNM; No locality data 1F BMNH; 1M FSCA; 1M MNHN; 2M USNM. **VENEZUELA**: *Mérida*, Mérida 3M BMNH; *Carabobo*, Las Quiguas 7M BMNH; Puerto Cabello 1M, 1F BMNH; 1M, 1F ZMHU; Valencia 1M BMNH; *Aragua*, Cata Cuyagua 2M, 2F AME; *Miranda*, Naiguatá, Caracas 1M, 1F AME; *Nueva Esparta*, Isla de Margarita 8M BMNH; 1M AME; *Bolívar*, Suapure 1M, 3F MCZ; *Amazonas,* Caño Tchuri 2F AME; Cerro de la Neblina 2F USNM; No locality data 1M, 2F BMNH; 1F MNHN. **COLOMBIA**: *Chocó*, Río San Juan 1M ZMHU; *Antioquia*, Valdivia 1M BMNH; across Río Magdalena from Barranca Bermejo 3M, 3F AMNH; *Bolívar*, El Banco 1F BMNH; *Magdalena*, San Lorenzo, Sierra Nevada de Santa Marta 1M, 1F

JHKW; *El Cesar*, Lake Zapatosa, Chiriguaná 1M BMNH; *Caldas*, Victoria 1F USNM; *Cundinamarca*, Bogotá 2M, 1F BMNH; *Valle del Cauca*, Cali 1F BMNH; 1M MNHN; above Jamundi (1300m) 2M USNM; Cañas Gordas (1000m) 29M, 13F AME; Espejeulo 1F BMNH; Miranda 1F USNM; Río Dagua 1F BMNH; Pance (3000ft) 7M, 3F FSCA; 8M, 6F USNM; *Tolima*, El Sapo 1M AME; Río Magdalena 1M ZMHU; *Cauca*, Popayán 1F BMNH; 1M ZMHU; Madre Vieja Hcda. Ukzania, Corinto 2M USNM; No specific locality 1M BMNH; *Meta*, San Martín 1M BMNH; Villavicencio 1F MNHN; Río Negro 1F AMNH; *Caquetá*, Sta. Rita 2M, 2F BMNH; *Putumayo*, Puerto Umbria 1F MNHN; ? Caucathal 3M, 3F MNHN; No locality data 1M, 1F ZMHU; 1M AMNH. **ECUADOR**: *Manabí,* Cojimies 1F USNM; *Pichincha,* Tinalandia (Jul) 2M FSCA; *Los Ríos,* Babahoyo 1M BMNH; Vinces 2M USNM; *El Oro,* Portovelo 1M AMNH; *Loja,* Qbda. Curichanga, 10 km E. of Macara (Mar) 2M, 1F JHKW; *Napo,* Río Tiputini, Coca-Tiguino rd. (Jul) 1M JHKW; Misahualli (Nov) 1M DA; km 4 Misahualli-Puerto Napo rd. (Oct) 2M RCB; Puerto Napo (Oct) 1F GWB; Tena (Jul) 2F JHKW; km 4 Tena-Pano rd. (Sept) 1F DA; Finca San Carlo (Feb, Apr, Sept) 6M JHKW; No locality data 1M, 1F BMNH; 1M MCZ. **PERU**: *Cajamarca*, nr. Hcda. Monte-Seco, 1 km N. of Puente Papayo (May) 1F MUSM; *Loreto*, Iquitos 1M, 2F MNHN; 1M AMNH; *San Martín*, Chazuta 1M MNHN. **BOLIVIA**: *Santa Cruz*, Buena Vista 1M, 1F BMNH. **BRAZIL**: *Amazonas*, Ipiranga 1M MNHN; Manaus 1F MNHN; Massauary 1M ZMHU; *Pará*, Itaituba 1M ZMHU; Pará 2M, 1F BMNH; Amazonas 1M BMNH; *Maranhão*, Miritiba 1F AME; *Distrito Federal*, Brasília 1F ZMHU; *Paraiba*, João Pessoa 7M, 3F USNM; 1M DA; ? S. Brazil 1F BMNH. **GUYANA**: *Cuyuni/Mazaruni*, Kartabo, Bartica 1F AMNH. **FRENCH GUIANA**: *Saint Laurent du Maroni*, Saint Laurent du Maroni 2M BMNH; 1F MNHN; No locality data 1M, 1F BMNH. **NETHERLANDS ANTILLES**: *Curaçao*, Hato Field 7M, 4F USNM; 1M, 1F AMNH; *Bonaire*, Dos Poos 2M AMNH.

TRINIDAD: Caparo 1F BMNH; St. Annes 3M, 1F MNHN; Hololo 1M AMNH; Aripo rd. 1F AMNH; No locality data 1F AME; 1F AMNH. **TOBAGO**: No locality data 3M, 2F BMNH. No locality data 5M, 9F BMNH; 1M, 4F ZMHU; 1F AME; 2M, 1F MNHN; 1M, 1F USNM; 1F MCZ.

Theope eupolis Schaus, 1890

Figs. 3h,i; 44a-d; 111; 179; 239; 268.

Theope eupolis Schaus, 1890. *Ent. Amer.* 6(1): 19. **TL**: Paso de San Juan, Mexico. Syntype male and females USNM [Examined]; Lectotype male USNM [Designated].

= ***Theope diores*** Godman & Salvin, 1897. *Trans. ent. Soc. Lond.* 45(2): 246. **TL**: Colima and Jalapa, Mexico. Syntype male BMNH and syntype male ZMHU [Examined]. **[n. syn.]**

= ***Theope talna*** Godman & Salvin, 1897. *Trans. ent. Soc. Lond.* 45(2): 245. **TL**: Roatán Is., Honduras. Holotype female BMNH [Examined]. **[n. syn.]**

Identification and Taxonomy: Average forewing length: both sexes 17mm.

MALE: *T. eupolis* is very similar to *T. virgilius* but can usually be distinguished on the dorsal surface by having blue that is restricted to the very base of the forewing, and which leaves a variably sized black area at the center of the distal hindwing margin (this may be almost absent or occupy most of the distal margin). The male genitalia of the two species are not significantly different.

FEMALE: females have equally variable amounts of dorsal blue but can also usually be distinguished from *T. virgilius* by the above characters as well as by the purplish hue to the dorsal coloration and the typical absence of a subapical blue forewing patch.

Schaus, and Godman and Salvin, working during the same period on different sides of the Atlantic seemed to know little of each other's taxonomic efforts and, in a typical scenario, Godman and Salvin (1897) described two synonyms of the older Schaus name *T. eupolis*. The first, *diores*, was described from two males without any mention of *T. eupolis* in the original description and the second, *talna*, was similarly described, from a single female. The type of *talna* has the same dark cinnamon colored ventral surface as *T. eupolis* and same arrangement of hindwing tornal spots, and a very similar dorsal pattern of reduced blue on both wings, although blue along the costal margin is atypically reduced. I believe that *talna* is merely a rather weakly marked female of *T. eupolis* that falls at the extreme boundary of variation for the species, and is therefore its junior synonym. The population of *T. eupolis* from Isla de Roatán, Honduras, whence *talna* was described, has perhaps, in isolation, evolved some genetic differences from mainland populations but their phenotypic manifestation is certainly not great enough to warrant subspecific recognition for *talna* (see introductory "Biogeography" section).

Since *T. eupolis* was described from both male and female specimens, and females are often very difficult to distinguish from those of *T. virgilius*, it would seem prudent to designate a male syntype as a lectotype. I choose a male syntype in the USNM that bears the following labels: "Theope/eupolis/type Sch.", "Type No./18776/U.S.N.M.", "l.g.6.".

Biology: Very little is known about the biology of this species, but label data suggest that it predominantly occurs in seasonally drier semi-deciduous and moist forest habitats up to at least 1100m. Beutelspacher (1982) reports that in Jalisco, Mexico, *T. eupolis* (as *T. diores*) occurs from October to December; here he found the species flying in the branches of a tree at 1800h (note the relevance of the high latitude of this locality in the late flying time).

Distribution: *T. eupolis* occurs from central Mexico to Panama, although it appears to be considerably more common in the north and west of its range. The following additional localities are listed by Warren *et al.* (1998 - *Co*) (as *T. diores*), Vargas *et al.* (1996 - *Ja*), Balcázar (1993- *Mi*) (as *T. diores*), and Raguso & Llorente (1992 - *Ve*) for MEXICO: *Colima*, Agua Dulce, La Salada, Platanarillos; *Jalisco*, Boca de Tomatlán, Chico's Paradise, Mismaloya; *Michoacán*, Pedernales; *Veracruz*, Laguna Encantada; by Ross (1964b) (as *T. diores*) for BELIZE: *Stann Creek*, Melinda; and by DeVries (1997) for COSTA RICA: *Heredia*, Magsaysay.

Specimens Examined: 76M 66F

MEXICO: *San Luis Potosí*, nr. Villa Juarez 1F USNM; *Jalisco*, Banderas Bay 1M AMNH; Chamela Bay 1M AMNH; Tenacatita 1F AMNH; *Colima*, Colima 1M BMNH; 1M ZMHU; Comala 6M, 2F AME; Manzanillo 1F USNM; *Michoacán*, Apatzingan 1F MCZ; *Morelos*, Huajintlan 1M AME; *Guerrero*, Acahuizotla (3500ft) 1M BMNH; 6M, 2F AME; Tierra Colorada 1F BMNH; 1M AME; Mexcala 1M AME; Puerto Marquez 1F AME; 1F AMNH; 2 mi. N.W. of El Treinte 2F AME; 3M, 4F AMNH; 5 km N.W. of Cadus 2M, 15F USNM; Zihuatenejo 1M AMNH; Acapulco 1M, 1F MCZ; 3M AMNH; No specific locality 1M USNM; *Oaxaca*, Candelaria Loxicha 1F USNM; Chiltepec 1F AMNH; *Veracruz*, Veracruz 1M FSCA; Rinconada 1M BMNH; Tocoy 1F BMNH; Punta Anton Lizardo 1M, 1F AME; Catemaco 1F AME; Soteapán 1M AME; Presidio 1M AME; Paso de San Juan 1M, 2F USNM; Jalapa 2M, 1F BMNH; 1M AMNH; No specific locality 2M AME; *Chiapas*, Tapachula 1M AME; Campet 1M AME; Santa Rosa, Comitan 1M AME; No locality data 2M, 1F MNHN; 2M, 1F USNM; 1M, 1F AMNH. **BELIZE**: *Toledo*, Punta Gorda 1M BMNH; Colombia 1M AMNH; No locality data 1M MNHN. **GUATEMALA**: *Quezal-Tenango*, Volcán de Santa María 1M BMNH; *Retalhuleu*, San Sebastian 1M, 4F USNM; *Escuintla*, Escuintla 1F USNM; *Santa Rosa*, Guazacapán 3M, 2F BMNH; No locality data 1M MNHN. **EL SALVADOR**: *La*

Libertad, La Libertad 1M AME; *La Paz*, 53 km E. of San Salvador 1M FSCA; San Esteban Catarina 1F AME. **HONDURAS**: *Cortés*, San Pedro Sula 2M, 2F BMNH; *Islas de la Bahía*, Isla de Roatán 1F BMNH; 2M MCZ; Isla de Bonacca 1M MCZ; *Olancho*, Patuca 1M AMNH; No locality data 1F BMNH; 1M, 2F ZMHU; 1F USNM. **NICARAGUA**: *Managua*, 15 km S. of Managua 2M, 1F AME; *Chontales*, No specific locality 1F BMNH. **COSTA RICA**: *Guanacaste*, Parque Santa Rosa 1M USNM; *Alajuela*, No specific locality 2F USNM. **PANAMA**: No locality data 2M USNM; 1F MCZ. No locality data 1F AME; 2M MNHN; 1F USNM. Mislabelled: Venezuela 1M BMNH.

GROUP XI: "*terambus* group"

Theope nobilis Bates, 1868 [stat. rev.]

Figs. 45a,b; 112; 180; 269.

Theope nobilis Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 410. **TL**: Rio Tapajós, E. Brazil. Syntype male and female BMNH [Examined]; Lectotype male BMNH [Designated].

Identification and Taxonomy: Average forewing length: male 16.5mm.

MALE: cladistic analyses (see introductory "Taxonomy" section) indicate that *T. nobilis* is evolutionarily intermediate between "*virgilius* group" species and "*terambus* group" species. However, most characters, including a postdiscal area of pale brown androconial scaling on the DFW, the presence of an aedeagal cornutus and medial posterior extension to the vinculum of the male genitalia, a small pointed projection from the lower posterior corner of the last tergite, and a reduced last sternite, unite *T. nobilis* with the "*terambus* group". Within both species groups, the pale yellow ventral surface is diagnostic. No other species with a yellow ventral surface, such as those in the "*pedias*" and "*sericea* groups", has black tornal spots on the VHW with bluish-white proximal scaling.

FEMALE: the syntype female of *T. nobilis* is actually a female *T. virgilius*. However, during correspondence about rare and unidentified riodinids with C. Brévignon and J.-Y. Gallard in French Guiana, I was able to identify one of their photographs of a female *Theope* as that of the true *T. nobilis*. It differs from the male by having more rounded wings, blue on the DFW that, although it is of the same pattern, only extends two-thirds of the way along the anal margin, and no blue distal to the discal cell or above on the DHW; it is the only known "*terambus* group" female to lack a subapical blue patch on the DFW. It is the only female specimen I have seen. It can immediately be distinguished from superficially similar females, such as those of *T. mundula*, *T. dabrerai* and *T. sericea*, by the spots in the tornus of the VHW.

The taxon *nobilis* was described by Bates (1868) as a full species from a single worn male and a female. On the male syntype specimen, the postdiscal pale brown androconial scaling on the DFW is barely visible and the ventral surface is highly rubbed giving the impression of a dirty yellow-brown ground color. It is therefore somewhat understandable why Stichel (1911) placed *nobilis* as a subspecies of *T. virgilius*, where it has remained until the present, especially since the female syntype does indeed represent *T. virgilius*. Given the gross morphological and wing pattern differences between the two species, as evidenced here by the illustration of a good quality male specimen of *T. nobilis* and the male genitalia of the lectotype, *nobilis* is returned to the rank of species. Given the mixed type series, it is necessary to designate the male syntype as a lectotype. This specimen in the BMNH bears the following labels: "nobilis", "Theope/nobilis,/Bates./Godman-Salvin/Coll. 1914.-5.", "Tapajos,/Amazons./H.W. Bates.", "Type/H.T.".

Biology: Nothing is known about the biology of this very rare species which is represented in collections, to my knowledge, by only three specimens.

Distribution: *T. nobilis* is only known to occur in the lower Amazon and Guianan regions.

Specimens Examined: 2M

BRAZIL: *Pará*, Rio Tapajós 1M BMNH. **FRENCH GUIANA**: No locality data 1M BMNH.

Theope sanjuani D'Abrera, 1994

Figs. 46a,b; 113; 181; 269.

Theope sanjuani D'Abrera, 1994. *Butts. Neotropical Region, Part VI*: 999, figs. **TL**: Río San Juan, W. Colombia. Holotype male BMNH [Examined].

Identification and Taxonomy: Average forewing length: male 15mm.

MALE: *T. sanjuani* is very similar to *T. publius*, but differs by having a more rounded wing shape, more indistinct dark brown postdiscal bands on the ventral surface that begin at the costa and then fade away, blue at the costal margin of the DHW and in cell M3 of the DFW immediately distal to the postdiscal pale brown androconial scaling, highlighting this region, and by lacking a small subapical blue patch on the DFW. The male genitalia of the two species do not differ significantly but the last abdominal tergite of *T. sanjuani* has a more elongate, broadly triangular projection from the lower posterior corner.

FEMALE: unknown.

Biology: Nothing is known about the biology of this species except that it does occur sympatrically with its sibling congener *T. publius*. It has not been collected in recent times.

Distribution: Unfortunately, a high proportion of *T. sanjuani* specimens bear no precise locality data and the species is currently known only from the type locality of Río San Juan in central-west Colombia. However, it is certain to occur throughout the Chocó region of west Colombia and north-west Ecuador and possibly the Darién of extreme eastern Panama.

Specimens Examined: 13M

COLOMBIA: *Chocó*, Río San Juan 5M BMNH; 3M ZMHU; No locality data 1M USNM; 1M AMNH; 1M MCZ. No locality data 1M ZMHU; 1M MNHN.

Theope publius C. & R. Felder, 1861

Theope publius publius C. & R. Felder, 1861

Figs. 47a-d; 114a; 182a; 240; 269.

Theope publius C. & R. Felder, 1861. *Wien. ent. Monats.* 5(4): 98. **TL**: Venezuela. Syntype female BMNH [Examined].

Identification and Taxonomy: Average forewing length: both sexes 16mm .

MALE: *T. publius* differs from the allopatric *T. syngenes* and *T. terambus* by having more vertically oriented ventral medial bands and a small subapical blue patch on the DFW. This last character also separates *T. publius* from the very similar and partially sympatric *T. sanjuani*; *T. publius* additionally differs by having a more pointed wing shape, no blue immediately distal to the pale brown postdiscal scaling on the DFW, additional blue at the costa of the DHW and more prominent ventral medial bands that extend all the way to the anal margin on each wing.

FEMALE: the female is similar to that of *T. syngenes* but differs by having a vertical medial band on the VFW, as in the male, slightly more blue at the anal margin of the DFW and usually a larger subapical blue patch on the DFW.

Biology: This species occurs from sea level to about 1000m in a variety of habitats from very wet rain forest to drier semi-deciduous woodland. In the former environment it appears to be present all year, but in the seasonally dry zone of south-west Ecuador and north-west Peru, it may fly only in the wetter months of December to May or at least be more common at this time. As with *T. virgilius*, specimens of *T. publius* from these areas tend to have paler brown ventral ground colors that probably help them to better match the substrate background when at rest. Males are typically found perching as solitary individuals about 2 to 4 meters above the ground in forest lightgaps and along forest edges and streamsides from about 1300 to 1500h.

L. Gilbert (in DeVries, 1997) is reported to have collected a female that was ovipositing near an *Azteca* ants nest. DeVries (1997) illustrates a caterpillar being tended by *Azteca* ants (Dolichoderinae) which he partially reared from an egg he believed was laid by a *T. publius* female (that he was unable to capture). The caterpillar is similar to that of *T. bacenis*, but it has only two very thin, broken lines either side of the dorsum and a smaller cluster of shorter balloon setae on the prothoracic shield.

Distribution: This subspecies ranges from Nicaragua to north Venezuela and north-west Peru. Although a few specimens are known from east of the Andes in northern Venezuela, *T. publius* certainly does not occur in the Amazon basin, and the two specimens in the BMNH and AMNH from the Amazon are mislabelled. The following additional localities are listed by DeVries (1997) for COSTA RICA: *Guanacaste*, Río Piedras de Cañas;

Alajuela, Florencia de San Carlos; *San José*, Santa Rosa de Puriscal; *Puntarenas*, Rincon de Osa, Manuel Antonio, Sirena; and are reported to me by C. Jiggins (pers. comm.) from ECUADOR: *Loja*, Tambo Negro.

Specimens Examined: 85M 49F

NICARAGUA: *Managua*, 15 km S. of Managua 2M, 1F AME; No locality data 1M BMNH. **COSTA RICA**: *Guanacaste*, Cañas 1M USNM; *Limón*, Limón 1M BMNH; Cahuita 1F USNM; *Puntarenas*, Golfito 1M USNM. **PANAMA**: *Chiriquí*, Bugaba 2M BMNH; 2M, 2F ZMHU; 1M USNM; Lino 1M MNHN; No specific locality 1F USNM; *Veraguas*, Isla de Coiba 1M USNM; Calovébora 1M USNM; *Panamá*, El Llano 1M, 1F USNM; Pacora 1M MNHN; Gamboa 1M USNM; Panama City 1M FSCA; Cerro Jefe 1M USNM; *Canal Zone*, Colón 1M USNM; Piña 5F AME; 2F FSCA; 1M DA; Curundu 1F AME; Diablo 1F AME; Gamboa 1M AME; Gatun 1F AME; 1M USNM; 3F AMNH; Miraflores 1F FSCA; Los Ríos 1M FSCA; 3M AME; 14M, 1F USNM; Summit Gardens 1M, 1F USNM; 1F AME; Cocoli 1F USNM; Paraiso 1M USNM; 1M AME; Madden Forest 1M USNM; No specific locality 1F AMNH; No locality data 4M, 1F BMNH; 3M, 2F ZMHU; 1M, 1F FSCA. **VENEZUELA**: *Mérida*, Mérida 3M, 1F BMNH; *Carabobo*, Valencia 1F ZMHU; *Distrito Federal*, Macuto 1M BMNH; La Guaira 1M ZMHU; *Aragua*, Cata Cuyagua 1F AME; Puerto Cabello 1F ZMHU; *Nueva Esparta*, Isla de Margarita 7M, 3F BMNH; *Bolívar*, Suapure 1F MCZ; No locality data 2M BMNH. **COLOMBIA**: *Chocó*, Río San Juan 1M ZMHU; *Antioquia*, across Río Magdalena from Barranca Bermeja 1F AMNH; *El Cesar*, Lake Zapatosa, Chiriguaná 1M BMNH; *Valle del Cauca*, Cali 1F BMNH; Cañas Gordas (1000m) 4M, 1F AME; No specific locality 1M BMNH; *Tolima*, Río Frio, Magdalena Valley 1M, 1F BMNH; ? Caucathal 1F MNHN; No locality data 1F BMNH; 1M USNM. **ECUADOR**: *El Oro*, Arenillas 1F BMNH; *Loja,* Qbda. Curichanga, 10 km E. of Macara 2M (Mar, May) JHKW. **PERU**: *Cajamarca*, nr. Hcda. MonteSeco, 1 km N. of Puente Papayo 1F MUSM. Mislabelled: Amazons 1F BMNH; Upper Amazon 1M AMNH. No locality data 2F ZMHU; 1M AME; 5M, 1F MNHN.

Theope publius incompositus Hall, **new subsp.**

Figs. 47e-i; 114b; 182b; 269.

Description: MALE: forewing length 17mm. Forewing pointed, hindwing slightly angular and pointed at tornus. *Dorsal surface*: forewing ground color black; blue occupies base of costa, all but distal end of discal cell, all but thin distal margin of cells above and below vein 1A+2A, three-quarters of lower half of cell Cu1, and forms a diagonal subapical line in cells M2-Rs; roughly ovoid area of pale brown postdiscal scaling occupies basal portions of cells Cu1-M1. Hindwing ground color blue, pale gray-brown at anal margin; black occupies thin distal margin, distal upper corner of cell M1 and entire area above vein M1, except for some blue scaling in distal portion of cell Rs. *Ventral surface*: forewing ground color pale chestnut-brown, paler at anal margin; discal cell end marked with a dirty white line; dark chestnut-brown, diagonal postdiscal band extends from costal margin to just below vein Cu2, broadening distally in cells M2 and M1; indistinct, slightly darker brown submarginal band extends from cell Rs to upper half of cell Cu2; very distal margin slightly darker chestnut-brown. Hindwing ground color pale chestnut-brown; dark chestnut-brown, postdiscal band extends prominently from vein Sc+R1 to vein Cu2, becoming faint in cell Cu2, and at middle is markedly displaced proximally inside discal cell; indistinct, slightly darker brown submarginal band occupies roughly ovoid area in apex between costal margin and vein Cu1, and at middle extends proximally as far as discal cell end; two black spots at submargin of cell Cu2 with bluish-white scaling distally and proximally, outer spot larger; very distal margin slightly darker chestnut-brown. *Head*: Ventral surface of labial palpi pale brown, dorsal surface dark brown. Eyes bare and brown, margins pale brown. Frons pale brown. Antennae black with white ventral scaling gradually decreasing from base to tip, entire inner edge broken sections of bare brown; clubs black; tips orange-brown. *Body*: Dorsal surface of thorax and abdomen blue, ventral surface pale brown. All legs pale brown. *Genitalia* (Figs. 114b; 182b): lower posterior corner of uncus triangular; elongate, triangular, posteriorly pointed extension from middle of vinculum; valvae narrow rectangles that are angled outwards in posterior view; tip of aedeagus elongate dorsally, a single triangular cornutus and a small rectangular sclerotised plate internally; last tergite with a small pointed projection from lower posterior corner; last sternite reduced to a small triangle that is attached to valvae and supports ventral surface of aedeagus.

FEMALE: differs from male in following ways: forewing length 18mm. Wing shape more rounded. *Dorsal surface*: ground color of both wings slightly paler; blue coloration on both wings paler, basal blue reduced on forewing, that in subapex of forewing whitish; more extensive black in cell M1 of hindwing, an ovoid black submarginal spot in cells Cu1-Rs, two in cell Cu2. *Ventral surface*: two elongate submarginal black spots in cell Cu2 of forewing, darker brown submarginal band of hindwing is disjointed, narrower, and extends to cell Cu1. *Genitalia*: see illustration for nominate *T. publius* (Fig. 240) from which it does not differ.

Types: *Holotype male*: MEXICO.- *Guerrero,* 2 mi. N. of El Treinte, 220m, 5 Sept 1967 (# 1605); in the AME.

Allotype female: MEXICO.- *Guerrero*, Acahuizotla, Jul 1959 (T. Escalante); in the AME. *Paratypes*: MEXICO.- *Guerrero*, same locality data as AT, 2 males: Oct 1956; 1 male: Apr 1957; 1 male: Oct 1957; 1 female: Sept 1958 (all T. Escalante); all in the AME.

Colima, 1 male: Colima, 1600ft, 9 May 1968 (R. Wind); 1 male: Comala, 2100ft, 12 Oct 1967 (R. Wind); 1 female: Comala, 2100ft, 13 Oct 1967 (R. Wind); all in the AME.

Etymology: The name of this taxon is derived from the Latin word "incompositus", meaning "disjointed", in reference to the disjointed nature of the transverse brown band on the ventral hindwing.

Diagnosis: Both sexes of *T. publius incompositus* subsp. n. consistently differ from the nominate by having a slightly distally displaced postdiscal band on the VFW and, most noticeably, a proximally displaced postdiscal band on the VHW that is further displaced inside the discal cell at its middle. Since this phenotype has a reasonably large geographic range, throughout which the aforementioned wing pattern characters are constant, and there is no evidence of clinal variation, I believe it warrants subspecific recognition. I would expect intergrades to occur in Honduras, whence no specimens are currently known.

Biology: The biology of this taxon is undoubtedly the same as that of the nominate.

Distribution: This subspecies occurs from central Mexico to El Salvador. Specimens in the BMNH from Venezuela are clearly mislabelled. The following additional localities are listed by Warren *et al.* (1998 - *Co*) and Vargas *et al.* (1996 - *Ja*) for MEXICO: *Colima*, 2 km W. of Chandiablo, Ojo de Agua, Suchitlán; *Jalisco*, Mismaloya; and by Austin *et al.* (1996) for GUATEMALA: *El Petén*, Tikal.

Specimens Examined: 44M 14F (1gynandromorph)

MEXICO: *Colima*, Colima 1M BMNH; 1M ZMHU; 1M AMNH; Comala 4M, 1F AME; *Michoacan*, Apatzingan 1M MCZ; *Guerrero*, Acahuizotla 8M, 2F AME; 2 mi. N. of El Treinte 3M, 3F AME; 1 mi. N.W. of Puerto Marquez 2M, 2F AMNH; Nochinde 1M AMNH; No specific locality 1M USNM; *Oaxaca*, 8 mi. E. of Tapanatepec 1M AME; *Veracruz*, Presidio 1F AMNH; *Chiapas*, Las Delicias 1F AME; *Campeche*, nr. Xpujil 1M

AMNH; *Yucatán*, Piste 1M AME; No locality data 1M ZMHU. **GUATEMALA**: *Retalhuleu*, San Sebastian 4M, 1F USNM; *Escuintla*, Escuintla 1M USNM; *Santa Rosa*, Guazacapán 1M BMNH. **EL SALVADOR**: *San Salvador*, Lago de Ilopango (500m) 1 gynandromorph AME. Mislabelled: Venezuela 3M BMNH. No locality data 7M, 2F BMNH; 1M, 1F AMNH.

Theope syngenes Bates, 1868

Figs. 48a-d; 115; 183; 241; 269.

Theope syngenes Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 409. **TL**: Santarem, E. Brazil. Syntype female BMNH [Examined]; Lectotype female BMNH [Designated].

Identification and Taxonomy: Average forewing length: both sexes 16.5mm.

MALE: *T. syngenes* is very similar to *T. terambus* and has an essentially identical dorsal surface. On the ventral surface it differs by having a darker chocolate brown square in the apex of the forewing with a very indistinct band beneath it, and a similar, variably present square near the apex of the hindwing with an indistinct band beneath it that often thickens at the anal margin; there are also usually two spots in the tornus of the VHW instead of one. Although the male genitalia of the two species are essentially indistinguishable and both species have variable wing patterns, *T. syngenes* occurs sympatrically with *terambus* throughout its range and consistently exhibits the above wing pattern differences. *T. syngenes* differs from the allopatric *T. publius* by having a broader wing shape, more diagonally oriented ventral postdiscal bands that on the forewing begin in the apex instead of mid-way along the costa, and a larger area of postdiscal pale brown androconial scaling on the DFW without a blue patch distal to it.

FEMALE: the female can be quite variable in the shape of the ventral bands and some specimens may have bands much like those of *T. terambus*, but the darker brown square in the apex of the VFW is always diagnostic. The dorsal blue coloration is also variable in extent, but is typically more reduced basally than in *T. terambus*; a small subapical blue patch is variably present.

Since there are no labelled syntypes of *T. syngenes* from Pará, one of the original type localities, and females of both *T. syngenes* and the very similar *T. terambus* exist in the BMNH from that locality, it would seem prudent to designate as a lectotype the labelled female syntype from the other type locality, Santarem, whence no *T. terambus* specimens originate, to avoid the possibility of a mixed type series. This specimen in the BMNH bears the following labels: "syngenes", "Theope/syngenes,/Bates./Godman-Salvin/Coll. 1914.-5.", "Santarem,/Amazons./H.W. Bates", "Type, H.T.".

Biology: Both sexes visit flowering trees at the forest edge throughout much of the day (R. Busby, pers. comm.; pers. obs.). No information is available on male perching times.

Distribution: *T. syngenes* has a broad range that extends from the base of the eastern Andes to the Atlantic but the vast majority of museum specimens originate from the lower Amazon and Guianan regions.

Specimens Examined: 15M 14F

ECUADOR: *Napo,* km 4 Misahualli-Puerto Napo rd. (Oct) 1M, 2F RCB; 1M, 1F GWB; Puerto Napo (Oct) 1M RCB; *Morona-Santiago,* Cuchentza, 1 km W. of Mendez (Sept) 1F JHKW. **PERU**: *Loreto*, Iquitos 1F AMNH. **BRAZIL**: *Pará*, Santarem 1F BMNH; Pará 2F BMNH. **GUYANA**: *Upper Takutu/Upper Essequibo*, Essequibo river 1M AMNH; *Cuyuni/Mazaruni*, Kartabo, Bartica 2F AMNH. **FRENCH GUIANA**: *Cayenne*, Cayenne

2M BMNH; 1M, 1F USNM; Mts. des Chevaux 2M USNM; Montsinéry 1M USNM; Galion 4M, 1F USNM; No locality data 1M, 1F BMNH. No locality data 1F BMNH.

Theope terambus (Godart, [1824])

Figs. 49a-d; 116; 184; 242; 269.

Polyommatus terambus Godart, [1824]. *Ency. méth.* 9 (Ins.) (2): 676. **TL**: "Java" [sic]. Types unknown.

= ***Psalidopteris lytaea*** Geyer, 1837. In: Hübner, *Zutr. Samml. exot. Schmett.* 5: figs. 901, 902. **TL**: Brazil. Types unknown; type illustration [Examined].

Identification and Taxonomy: Average forewing length: both sexes 17mm.

MALE: *T. terambus* can immediately be separated from the Central American species *T. bacenis* and *T. basilea* since it lacks any white markings in the basal half of the ventral surface. It is most similar to the partially sympatric *T. syngenes* which shares an identical dorsal pattern; *T. terambus* differs on the ventral surface by having medial bands of even width and intensity without any darker brown squares at the costal margins of each wing, and usually only one tornal hindwing spot instead of two. The male genitalia of the two species do not differ significantly.

FEMALE: some specimens may look very much like the females of *T. syngenes* with some darker brown shading in the apex of the VFW, but this shading is never formed into such a distinctive square shape; also *T. terambus* typically lacks submarginal brown spots on the VHW and has more blue on both dorsal wing surfaces.

Both sexes exhibit variation in size, the prominence and shape of the ventral bands and the hue of the ventral ground color, but since many phenotypes, and all manner of intermediates, appear to reoccur in disparate localities throughout the range of the species, the delimitation of subspecies is not appropriate. The original description of *T. terambus* in Godart ([1824]) is relatively long and accurate, but although he states that one female type is in the MNHN, I could not locate it, nor is it listed by Callaghan (1995) as occurring in that museum. The illustrations of *lytaea* in Geyer (1837) were correctly recognised as being synonymous with *T. terambus* by Stichel (1911).

Biology: Despite its good representation in collections, relatively little is known of the biology of this species. However, label data suggest that it is tolerant of disturbed, forest edge habitats, where G. Busby (pers. comm.) informs me that he observed a male visiting small white flowers. Callaghan (1983) also records *T. terambus* hilltopping at Villavicencio in eastern Colombia, from 1240 to 1445h.

Distribution: *T. terambus* is widespread throughout the Amazon and Guianan regions and occurs as far south as Argentina and Paraguay, suggesting its possible occurrence in Uruguay. It appears to be relatively common along the Atlantic sea-board of South America, but it is considerably rarer towards the base of the eastern Andes. The following additional localities have been reported to me by K. Willmott (pers. comm.) from COLOMBIA: *Meta*, Cubarral (ESM).

Specimens Examined: 103M 68F

VENEZUELA: *Nueva Esparta*, Isla de Margarita, La Sierra (500m) 4M, 2F USNM; *Delta Amacuro*, Río Aguirre 1F MNHN; *Bolívar*, Suapure 4M, 1F MCZ. **COLOMBIA**: *Meta*, Villavicencio 1M JHKW; *Caquetá*, Río Bodoquero (1300ft) 1F USNM; No locality data 1F USNM. **ECUADOR**: *Napo,* km 4 Misahualli-Puerto Napo rd. (Oct) 1M GWB; km 4 Tena-Pano rd. (Sept) 1M DA. **PERU**: *Loreto*, Iquitos 9M, 5F MNHN; *San Martín*, Juanjuí 1M MNHN; Chazuta 2M, 1F MNHN; *Junín*, No specific locality 1F BMNH; *Madre de Dios*, 10 km N. of Puerto Maldonado 1M USNM; ? Muchomaite 1F FSCA.

BOLIVIA: *Santa Cruz*, Buena Vista 750m 1F BMNH; Santa Cruz 1F BMNH. **ARGENTINA**: *Entre Ríos*, No specific locality 1M BMNH. **BRAZIL**: *Amazonas*, Tefé 1M BMNH; Ipiranga 1F MNHN; *Rondônia*, environs of Fazenda Rancho Grande, nr. Cacaulândia 1F NSM; *Pará*, Santarem 1F ZMHU; Itaituba 1M, 1F ZMHU; Pará 1M, 2F BMNH; *Mato Grosso*, Cuiába 1M BMNH; Chapada 1F BMNH; 1F AMNH; Diamantino 1M USNM; *Bahia*, Itabuna 1F AME; *Minas Gerais*, Leopoldina 1M ZMHU; Paracatu 2M USNM; Serra do Cipo 1M USNM; *Espírito Santo*, Santa Cruz 2M, 2F BMNH; Linhares 1M, 1F AME; Conceicão de Barra 1M AME; *Rio de Janeiro*, Paneiras 1M BMNH; 1M USNM; Rio de Janeiro 1M ZMHU; 8M, 6F BMNH; 1F MNHN; 2M AMNH; 1M MCZ; Gávea 1M MNHN; *Santa Catarina*, Joinvile 2M USNM; São Bento do Sul 1M AME; ? S. Brazil 2M MNHN; No locality data 2M, 3F BMNH; 1M MCZ. **PARAGUAY**: No locality data 1F BMNH. **FRENCH GUIANA**: *Cayenne*, Cayenne 1M BMNH; Montsinéry 1M USNM; Galion 1F USNM; 1M JHKW; Sinnamary, Crique Toussaint 1M USNM; Orapu 1F MNHN; *Saint Laurent du Maroni*, Saint Laurent du Maroni 1F BMNH; 1M USNM; 1M MNHN; No locality data 3F BMNH. **TRINIDAD**: St. Annes 1F BMNH; 1M, 2F AME; 8M, 1F MNHN; St. Georges 1M BMNH; Manzarilla 1F BMNH; Fondes Amandes 1F BMNH; 1M, 1F AME; 6 mi. N.W. of Arima 1F AME; Arima Valley 1M AMNH; Macqueripe Bay 1F AMNH; Santa Cruz Valley 1F AMNH; Maracas Bay 2F AMNH; Port of Spain 1M AME; 1M MNHN; Hololo 1M AME; 3M, 1F AMNH; No locality data 1F MNHN; 2M AMNH. No locality data 5M, 6F BMNH; 8M, 1F ZMHU; 1F USNM; 1M, 1F MNHN; 1M, 1F AMNH; 1M MCZ.

Theope bacenis Schaus, 1890

Figs. 7; 50a-h; 117; 185; 243; 269.

Theope bacenis Schaus, 1890. *Ent. Amer.* 6(1): 19. **TL**: Coatepec, Mexico. Holotype male USNM [Examined].

= ***Theope mania*** Godman & Salvin, 1897. *Trans. ent. Soc. Lond.* 45(2): 247. **TL**: San Blas, Mexico. Holotype female BMNH [Examined]. **[n. syn.]**

= ***Theope eleutho*** Godman & Salvin, 1897. *Trans. ent. Soc. Lond.* 45(2): 247. **TL**: Chiriquí, Panama. Holotype female ZMHU [Examined]. **[n. syn.]**

Identification and Taxonomy: Average forewing length: male 20mm, female 20.5mm.

MALE: *T. bacenis* is most similar to the partially sympatric *T. basilea* but throughout its geographic range can be distinguished by its falcate wing shape, its paler blue dorsal coloration that does not extend as far towards the tornus on the forewing, less prominent postdiscal brown androconial scaling on the DFW, by having a ventral ground color composed of more varied and often darker shades of brown, an additional round white spot at the base of the discal cell on the VHW and a series of smaller black spots on the VHW that extend around the entire submargin and occasionally into the tornal area of the VFW. Some specimens with less heavily marked ventral patterns may resemble *T. terambus*, but the larger number of spots at the submargin of the VHW and the white spots of the ventral discal cells are still diagnostic for *T. bacenis*. The male genitalia of all three species differ only marginally in the shape of the uncus and the valvae.

FEMALE: its wing shape and ventral pattern are diagnostic, but it can additionally be distinguished from the females of similar species by its brighter greenish-blue dorsal coloration. The signae of the female genitalia of *T. bacenis* are unusual in possessing numerous transverse creases, a character shared only with the sister species *T. basilea*.

T. bacenis is a geographically variable species and, unfortunately, its type specimen is a weakly marked, somewhat aberrant individual from one extreme of its range. Because of this and the fact that the holotype was deposited in a North American museum, early European taxonomists were ignorant of its identity and only seven years after its description, Godman & Salvin (1897) described two synonyms of it. The first, *mania*, was described from a single worn female specimen that matches well with the male holotype of *bacenis* and is even from the same geographical area.

The second, *eleutho*, was described from the other extreme of the species's range from a series of heavily marked specimens, and because these are more prevalent in collections, *bacenis* has been erroneously known for the past century under the name *eleutho* (e.g. DeVries, 1997). I deliberated about whether to retain *eleutho* as a subspecies of *bacenis*, but since, from museum specimens, it is clear that all wing pattern characters vary clinally, I decided against this. As the cline progresses southwards through Central America, the wing shape becomes more exaggeratedly falcate, the ventral ground color becomes darker and has more heavily contrasted elements, the medial band on both wings becomes more prominent and kinks more proximally near the apex of the forewing and at the anal margin of the hindwing, the round white spot at the base of each discal cell becomes larger and white lines appear at each discal cell end, and finally, the black hindwing spots extend further up the submargin and in some specimens appear in the tornal area of the forewing.

Biology: This species is recorded in lowland rain forest habitats below 600m in Costa Rica (DeVries, 1997), but at slightly higher elevations in premontane wet forest in Mexico (de la Maza and White, 1990; Warren *et al.*, 1998). Both sexes were recorded nectaring on *Cordia spinescens* in Veracruz, Mexico, by Ross (1976). No information is available on male perching times.

T. bacenis has been reared in Costa Rica on an unidentified *Inga* species (Leguminosae) (as *T. eleutho*) (DeVries *et al.*, 1994). DeVries (1997) describes the mature larva as having a reddish brown head capsule, with a centrally positioned inverted white "V", an extremely exaggerated corona of dark brown and black balloon setae on the prothoracic shield, a body that is brownish green on the dorsum and pale green laterally, with a dark brown band separating the two areas and short sparse ventro-lateral setae, and a conspicuously broad anal plate that is largely black with a marbled white pattern either side of a broad black medial band. The solitary caterpillars are tenaciously tended by *Azteca* ants (Dolichoderinae) and their tentacle nectary organs are conspicuously pink when everted. Pupation takes place inside a leaf that was curled by the caterpillar; the brown pupa is cylindrical, tapering somewhat from the head to the last abdominal segment, and unadorned (DeVries, 1997). DeVries (1997) should be consulted for a black and white drawing of the mature caterpillar and SEM's of its anal plate and balloon setae.

Distribution: *T. bacenis* is known to range with certainty from central Mexico to Panama, but a single specimen in the collection of E. Schmidt-Mumm (Bogotá) from the Villavicencio area of east Colombia, a point where the range of a number of Central American taxa ends, also suggests a broad Colombian range. Specimens with weakly marked ventral patterns (f. *bacenis*) occur from Mexico to El Salvador, while those with more heavily marked ventral patterns (f. *eleutho*) occur from Nicaragua (and probably Honduras) to Colombia. Although I have examined no specimens, Hoffmann (1940) additionally reports the ocurrence of this species in the Mexican states of Tabasco and Oaxaca. The following additional localities are listed by Warren *et al.* (1998 - *Co*) (as *T. mania*), Field (1940 - *Mi*) (as *T. mania*), and Raguso and Llorente (1992 - *Ve*) for MEXICO: *Colima*, Platanarillos, Suchitlán; *Michoacán*, Morelia, El Sabino; *Veracruz*, Laguna Encantada; by Meerman (1999) (as *T. basilea*) for BELIZE: *Stann Creek*, No specific locality; by DeVries (1997) (as *T. eleutho*) for COSTA RICA: *Puntarenas*, Sirena, Palmar Sur; and are reported to me by K. Willmott (pers. comm.) from COLOMBIA: *Meta*, Río Guayabero (ESM).

Specimens Examined: 48M 46F

MEXICO: *San Luis Potosí*, El Salto Falls 1M FSCA; 1M AME; Laurel Canyon, Río Axtla 1M AMNH; *Nayarit*, San Blas 1F BMNH; Compostela 1F AMNH; *Morelos*, Yautepec 1M AME; *Guerrero*, Acahuizotla 2M, 4F AME; No specific locality 1M BMNH; 1M, 1F USNM; *Veracruz*, Coatepec 1M USNM; 1M, 1F AME; Catemaco 1F AME; Presidio 1M AME; Cordoba 1M AMNH; Jalapa 1F USNM; Soteapán 1F AME; *Chiapas*, Tuxtla Gutierrez 2M FSCA; Santa Rosa, Comitán 1F AME. **BELIZE**: *Toledo*, Colombia 1M AMNH. **GUATEMALA**: *Ratalhuleu*, San Sebastian 2M USNM; *Suchitepéquez*, Pt. Xtacapa 1M USNM; *Escuintla*, Escuintla 1M USNM; Palín 2M USNM; *Guatemala*, San Pedro Yepocapa 1M AMNH; *Santa Rosa*, Barberena 4M, 1F BMNH; No locality data 3M, 1F MNHN. **EL SALVADOR**: *San Salvador*, Sta. Tecla (1100m) 5M, 2F AME; *Sonsonate*, San Isidro (1000m) 2M AME; *Cuscatlán*, San Ignacio, Chalatenango 1F AME. **NICARAGUA**: *Chontales*, No specific locality 1M BMNH. **COSTA RICA**: *Limón*, Limón 1F BMNH; *Cartago*, Turrialba (2000ft) 1F AME; 1F USNM. **PANAMA**: *Chiriquí*, Bugaba 2F ZMHU; No specific locality 3M, 3F ZMHU; 2F MNHN; *Veraguas*, Calobre 1M BMNH; *Panamá*, El Llano 1M, 1F USNM; Bayano 1M USNM; Río Parti 1F USNM; *Canal Zone*, Cocoli 2M, 1F AME; 1F USNM; Piña 2M, 2F USNM; 1M, 1F FSCA; 1M, 3F AME; Madden Forest 1M, 8F USNM; Ft. Clayton 1F USNM; Colón 1M AME.

Theope basilea Bates, 1866

Figs. 51a-d; 118; 186; 244; 269.

Theope basilea Bates, 1866. *Ent. mon. Mag.* 3: 155. **TL:** Lion Hill, Panama. Syntype female BMNH [Examined].

Identification and Taxonomy: Average forewing length: both sexes 19.5mm.

MALE: *T. basilea* differs from the allopatric *T. terambus* on the ventral surface by having a more uneven postdiscal forewing band, vein Sc+R1 of the hindwing outlined in dark brown, two white markings in the discal cell of the forewing and sometimes one at the discal cell end on the hindwing and two or three large hindwing tornal spots instead of one smaller one, as is usually found in *T. terambus*. It is most similar to its partially sympatric and geographically variable sister species *T. bacenis*, but can always be distinguished by its pointed instead of falcate wing shape, darker blue dorsal coloration that extends further towards the tornus at the anal margin of the forewing, more evenly colored ventral ground color, by lacking a white spot at the base of the discal cell on the VHW and by having larger spots at the submargin of the VHW that are restricted to the tornal area.

FEMALE: it has the same distinguishing ventral characteristics as the male, but is additionally separated from *T. terambus* by having more basally restricted blue on the DFW, with a larger and more proximally positioned subapical blue patch, and slightly reduced blue distally on the DHW with distinct submarginal black spots; and from *T. bacenis* by having pale blue instead of bright green-blue dorsal coloration that is again slightly more restricted basally.

Biology: In European collections, *T. basilea* is very rare, but in North American collections there are numerous specimens from Panama collected by G. B. Small and H. L. King. This observation, combined with my experience with the species in Ecuador, suggests that it can be locally common in lowland rainforest areas, and DeVries (1997) also reports it from semi-deciduous woodlands in Guanacaste Province, Costa Rica. In Ecuador, I found males perching in a hilltop lightgap, where they would arrive from the surrounding forest and perch on only a few specific leaves about 6 meters above the ground; they consistently flew between 1600 and 1715h each day, during which time they made frequent rapid sorties to defend their small territories. If one individual was removed, another would soon take its place, but only one was ever present at a time. DeVries (1997) observed both sexes visiting *Croton* flowers from 1000 to 1030h in Panama. Museum data labels indicate that *T. basilea* is present all year round, at least in Panama.

Distribution: *T. basilea* occurs from Costa Rica to western Ecuador, but the vast majority of specimens have been collected in Panama. The record of *T. basilea* from Belize by Meerman (1999) is certainly referrable to *T. bacenis*. The following additional localities are listed by DeVries (1997) for COSTA RICA: *Guanacaste*, Cañas; *Limón*, 5.8 km S. of Río Blanco; *Puntarenas*, Carrara, Río Catarata; and have been reported to me by K. Willmott (pers. comm.) from COLOMBIA: *Valle de Cauca*, Río Tatabro (JS).

Specimens Examined: 63M 51F

PANAMA: *Panamá*, El Llano 1M, 1F USNM; Río Parti 1F USNM; *Canal Zone*, Piña (all year) 20M, 19F AME; 3M, 4F USNM; 8M, 1F FSCA; Río Torti 1F USNM; Summit Gardens 1M USNM; 1F AME; Gatun 3M USNM; Cocoli 4M, 3F USNM; Madden Forest 10M, 9F USNM; Gamboa 1M, 2F USNM; 2M, 6F AME; 1M, 2F PJD; Lion Hill 1F BMNH. **COLOMBIA**: *Chocó*, San Pablo, Río San Juan 1M BMNH; 2M ZMHU. **ECUADOR**: *Esmeraldas,* Estacion Experimental La Chiquita (Dec) 1M JHKW; La Punta, km 44 Lita-San Lorenzo rd. (Jul) 5M JHKW.

GROUP XII: "*theritas* group"

Theope comosa Stichel, 1911

Figs. 55a-d; 119; 190; 245; 270.

Theope comosa Stichel, 1911. *Gen. Insectorum.* 112(B): 356, pl. 27, fig. 97. **TL**: Pebas, Peru. Holotype male ZMHU [Examined].

Identification and Taxonomy: Average forewing length: both sexes 15.5mm.

MALE: *T. comosa* is one of the most distinctive members of the "*theritas* group" and is its most plesiomorphic. It is perhaps most similar to *T. theritas* and *T. sobrina* but can be distinguished from these species and all others by its pointed hindwing, two highly distinctive black spots in the tornus of the VHW (a larger one at the tornal point with a smaller and often partly coalesced one above it), long androconial hairs at the anal margin of the VFW that are also visible on the dorsal surface, and variably present disjunct postdiscal blue spot on the DFW. Unlike other members of the "*theritas* group", the dorsum of the thorax and abdomen in *T. comosa* is densely covered with blue scales, a character that it shares only with members of the "*virgilius*" and "*terambus* groups". The male genitalia of *T. comosa* are unique in the group in having no posteriorly projecting upper "arm" to the vinculum and a unique, bulbously tipped aedeagus that has a small circular dorsal opening; the last tergite also has a uniquely broad and rounded projection from the lower posterior corner.

FEMALE: specimens representing the female of *T. comosa* have not been previously recognised as such, but were figured by D'Abrera as "*Theope* ? sp." (see Appendix A). Female *T. comosa* has a similar dorsal pattern to that of most "*theritas* group" species, especially *T. thootes* and *T. phaeo* but the two-tone orange and gray-brown ventral surface, which is so radically different to that of the male, easily separates it, but superficially gives it the appearance of a species in the "*pedias* group". The typically coalesced tornal spots on the VHW are, however, an important diagnostic character, one that provided an important clue to linking the sexes of one of the most strongly dimorphic *Theope* species.

Biology: This rare species occurs very locally in intact lowland rainforest habitats below 600m. In Ecuador, I have found males perching in forest lightgaps, especially along ridegtops, from 1230 until 1415h. At such a site on the upper Río Tiputini, only a single individual would be observed at any one time, but if it was removed, another would soon take its place.

Distribution: This species appears to be restricted to the upper Amazon basin.

Specimens Examined: 12M 5F

COLOMBIA: *Putumayo*, Upper Río Putumayo 1F MNHN. **ECUADOR**: *Napo,* Río Napo 1F BMNH; Campo Anaconda, nr. Coca (Apr) 1M JHKW; Río Tiputini, Coca-Tiguino rd. (Mar, Jul) 3M JHKW; *Morona-Santiago,* Taisha (Jun) 1M JHKW. **PERU**: *Loreto*, Pebas 1M ZMHU; Iquitos 1F BMNH; 1M MNHN; Río Cachiyacu, Iquitos 1F BMNH; Río Nanay 1M MNHN; Río Sucusari, Explornapo-Aceer 3M USNM; *Madre de Dios*, Parque Nacional del Manu, Pakitza 1M USNM. **BRAZIL**: *Rondônia*, environs of Fazenda Rancho Grande, nr. Cacaulândia 1F NSM.

Theope zostera Bates, 1868

Figs. 52a-d; 120; 187; 270.

Theope zostera Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 405. **TL**: São Paulo de Olivença, W. Brazil. Syntype female BMNH [Examined].

Identification and Taxonomy: Average forewing length: both sexes 12mm.

Sexes similar but female has a fractionally more elongate wing shape, more violaceous dorsal coloration and a less contrasted ventral surface, with larger and more indistinct markings around the discal cell ends. *T. zostera* is the most easily recognised species of the "*theritas* group". Its dorsal blue is more extensive than that of other species, occurring at the costal margin of the hindwing and extending further towards the distal margin of the forewing postdiscally in both sexes, as in only the females of other "*theritas* group" species, and its ventral pattern, with its contrasted elements of paler and darker brown, is most distinctive and reminiscent only of the otherwise dissimilar *T. christiani*. Despite such atypical wing pattern elements, the male genitalia of *T. zostera* are much like those of other members in the group, their most diagnostic feature being the symmetrical, medium-sized, triangular-shaped posterior projections of the vinculum. The right-hand projection of the last sternite is also longer than that of any other species except *T. sobrina*, and the last tergite is unusual for the group in lacking a long projection from the lower posterior corner, again similar only to that of *T. sobrina*.

Biology: Until very recently, *T. zostera* was only known from a handful of female specimens, but a number of males have now been collected in Ecuador and one is figured here for the first time. The species is very rare and local in intact lowland rainforest habitats up to 1000m. Two males were found perching about 6 meters above the ground in a ridgetop lightgap at 1230h. Another solitary male was encountered feeding on a low flowering bush in a hilltop lightgap at 1250h.

Distribution: This species appears to be restricted to a rather small area of the upper Amazon basin.

Specimens Examined: 7M 4F

ECUADOR: *Pastaza,* 14 km S. of Shell (1000m) (Oct) 1M RCB; *Napo,* Coca-Tiguino rd., Tiguino (Oct) 2M JHKW; Río Tiputini (Apr) 1M JHKW; Jatun Sacha (Oct) 1M DA; Apuya (Oct) 1M JHKW; 1M RCB. **PERU**: *Loreto*, Pebas 1F ZMHU; Río Sucusari, Explornapo-Aceer 1F USNM. **BRAZIL**: *Amazonas*, São Paulo de Olivença 1F BMNH; 1F ZMHU.

Theope nodosus Hall, **new sp.**

Figs. 53a,b; 121; 188; 270.

Description: MALE: forewing length 13mm. Base of forewing costa strongly convex, distal margin straight; hindwing tornus pointed, distal margin straight. *Dorsal surface*: forewing ground color black; blue occupies entire discal cell with some scaling above it, all but a thin black distal margin in cells above and below vein 1A+2A, and basal portions of cells Cu1-M1, distal edge of blue markedly concave. Hindwing ground color blue, anal margin gray; black along costal margin extends into upper distal portion of cell M1 then as thin line around distal margin. *Ventral surface*: both wings entirely pale gray-brown except for pale gray area at anal margin of forewing and slightly darker, indistinct line at very distal margin of both wings. *Head*: Dorsal surface of labial palpi dark brown, ventral surface pale gray-brown. Eyes bare and brown, margins white. Frons pale brown with dark brown medial stripe. Antennae black with white scaling ventrally at base of each segment, entire inner edge broken sections of bare brown; clubs black; tips orange-brown. *Body*: Dorsal surface of thorax and abdomen black, ventral surface gray-brown. All legs pale brown. Genitalia (Figs. 121; 188): lower posterior corner of uncus triangular; falci compact and rectangular at base; short, narrow and pointed posterior projection from upper portion of vinculum (symmetrical on either side); valvae consist of rounded basal portion and elongate posteriorly projecting portion; aedeagus curves upwards into extended, sinuate, anteriorly pointing tip, vesica studded with tiny sclerotised structures in right-hand view only; pedicel asymmetrical. Last tergite is narrower anteriorly and has small, asymmetrical triangular projection from each lower posterior corner; last sternite greatly reduced ventrally but highly modifed dorsally into a large asymmetrical structure consisting of a long club-shaped left-hand portion and short, rounded right-hand portion, connects to genital armature.

FEMALE: unknown.

Types: *Holotype male*: ECUADOR.- *Napo Prov.,* km 12 Tena-Puyo rd., Finca San Carlo, 600m, 20 Feb 1995 (J. P. W. Hall); to be deposited in the BMNH.

Paratypes: ECUADOR.- *Napo Prov.,* 1 male: same locality data as HT, 14 Apr 1995 (J. P. W. Hall); 1 male: km 20 Tena-Puyo rd., Apuya, 600m, 13 Oct 1996 (K. R. Willmott); both in the coll. of JHKW.

Etymology: The name of this species is derived from the Latin word "nodosus", meaning "gnarled", in reference to the twisted tip of the aedeagus of its male genitalia.

Diagnosis: *T. nodosus* is superficially very similar to a number of other "*theritas* group" species. It is smaller than *T. thootes* and *T. sobrina*, and has a paler ventral surface and an entirely blue discal cell on the DFW, thus most closely resembling *T. apheles*. *T. nodosus* differs from *T. apheles* by having a slightly paler ventral surface, a straight instead of convex distal forewing margin, an entirely blue discal cell on the DHW without any pale brown scales intruding over its costal edge, and typically a more concave distal edge to the blue of the DFW (although the male lectotype of *T. apheles* has a similar pattern of forewing blue to *T. nodosus*). Worn or atypically patterned male specimens of *T. nodosus* will always be easily identified by examining the genitalia (see Appendix B for extensive list of dissections made in this species group). The posterior projections of the vinculum are symmetrical and much shorter than those of *T. thootes* and *T. apheles*, more closely resembling those of *T. sobrina*, but *T. nodosus* does not have the spiky valvae or spiky, symmetrical last sternite of that species. The sinuate, anteriorly projecting tip to the aedeagus is a diagnostic autapomorphy for *T. nodosus.*

Biology: This species is a very rare and local inhabitant of intact lowland rainforest, where solitary males were encountered perching in hilltop lightgaps between 1115 and 1400h. Adults are present during both wet and dry seasons.

Distribution: *T. nodosus* is currently known only from the base of the eastern Andes in Ecuador but it undoubtedly has a broader west Amazonian distribution.

Specimens Examined: 3M

ECUADOR: *Napo*, Finca San Carlo (Feb, Apr) 2M JHKW; Apuya (Oct) 1M JHKW.

Theope phaeo Prittwitz, 1865

Figs. 56a-f; 123; 191; 246; 271.

Theope phaeo Prittwitz, 1865. *Stett. ent. Ztg.* 26: 312. **TL**: Rio de Janeiro, S.E. Brazil. Syntype male ZMHU [Examined].

= ***Theope theutis*** Godman & Salvin, 1886. *Biol. centr.-amer., Lep. Rhop.* 1: 483; 3: pl. 46, figs. 16, 17. **TL**: Polochic Valley, Guatemala, and Chontales, Nicaragua. Syntype male and females BMNH [Examined]. **[n. syn.]**

= ***Theope folia*** Godman & Salvin, 1886. *Biol. centr.-amer., Lep. Rhop.* 1: 483; 3: pl. 47, figs. 23, 24. **TL**: Peña Blanca (3000-4000ft), Panama. Holotype male BMNH [Examined]. **[n. syn.]**

Identification and Taxonomy: Average forewing length: both sexes 14mm.

MALE: *T. phaeo* has a dorsal surface that is typical of "*theritas* group" species but a diagnostic falcate wing shape and ventral pattern, that consists of a pale gray ground color overlayed with darker gray-brown extending along the basal two-thirds of each costal wing margin and then traversing two-thirds of each wing towards the anal margin, and usually two or three small black spots in the tornus of the hindwing. The asymmetrical vinculum of the male genitalia is unique in the group in having a long upper posterior projection from the left-hand side but none from the right-hand side.

FEMALE: the characteristic ventral pattern of the male is often very faded and barely discernible in the female, making it easily confused with the females of other "*theritas* group" species, with which Amazonian specimens of *phaeo* are often miscurated in collections. It is especially similar to *T. sobrina* but can be distinguished from this species by its falcate wing shape, that incidentally leads to a longer gap between the tip of the hindwing tornus and the end of the anal fold; the variably present black spots in the tornus of the VHW and darker ventral ground color additionally separate it from *T. thootes* and *T. apheles*. The female genitalia of *T. phaeo* are utterly distinct from those of all the aforementioned species, differing most notably by having a rounded ostium bursae without any dorso-lateral projections, and a completely unsclerotised ductus bursae.

Both sexes of *T. phaeo* vary widely over the large geographic range of the species. In males, this variation includes the extent to which the ventral pattern elements are contrasted, the extent (or even absence) of pale brown scaling in the upper half of the discal cell on the DHW, the shape of the uncus, upper "arm" of the vinculum, aedeagus and valvae of the genitalia, and the shape of the last sternite and tergite; in both sexes, it includes the presence or absence of black spots in the tornus of the VHW, the shade of ventral ground color and the extent of blue coloration on the DFW, especially in females. Specimens from certain geographic localities do tend to exhibit specific wing pattern characters; for example, west Ecuadorian specimens tend to have the most highly contrasted ventral patterns and Amazonian specimens tend to have slightly darker blue dorsal coloration, but most extreme character developments recur throughout the range of the species and are connected by multidirectional clines. Thus, no one sufficiently discrete phenotype occurs over a large enough area to warrant any subspecific divisions.

Bearing the above in mind, it is not surprising that synonyms of *T. phaeo* have been described; Godman and Salvin (1886) described two in the same work from Central America without mentioning *T. phaeo* in the original description of either. Both *theutis*, retained by Stichel (1930) and subsequently Bridges (1994) as a distinct species, and *folia*, which was placed as a subspecies of *T. phaeo* by Stichel (1911), fall within the normal variation exhibited by *T. phaeo*.

Biology: *T. phaeo* has one of the broadest altitudinal ranges of any *Theope* species and has been recorded from sea level to about 1600m. In eastern Ecuador, I found a small number of males perching in a forested ridgetop lightgap between 1315 and 1400h. Both sexes feed on flowering trees and bushes at the forest edge and along streamsides.

Distribution: *T. phaeo* is widespread, occurring from Mexico to western Ecuador and throughout the Guianan and Amazon regions as far south as south-east Brazil. It is considerably more common in areas to the west of the Andes, and apparently very rare in south-east Brazil. The following additional localities are listed by DeVries (1997) for COSTA RICA: *Heredia*, Bajo Rodriguez; and are reported to me by J.-Y. Gallard (pers. comm.) from BOLIVIA: *Cochabamba*, Villa Tunari.

Specimens Examined: 68M 61F

MEXICO: No locality data 1F BMNH. **GUATEMALA**: *Alta Verapaz*, Río Polochic Valley 1F BMNH. **HONDURAS**: *Cortés*, La Cambre 3M, 2F BMNH. **NICARAGUA**: *Atlántico Sur*, Bluefields 2M AME; *Chontales*, No specific locality 1M, 2F BMNH; No locality data 2F BMNH. **COSTA RICA**: *Alajuela*, Miravalles 1M BMNH. **PANAMA**: *Chiriquí*, Potrerillos (3600ft) 1M AME; 1M, 4F USNM; *Coclé*, Cerro Peña Blanca (3000-4000ft) 1M BMNH; *Panamá*, Altos de Pacora 1M, 1F USNM; El Llano 2M, 3F USNM; Cerro Campana (1500ft) 4F AME; 5M, 2F USNM; Cerro Jefe 1F USNM; *Canal Zone*, Piña 1F FSCA; 1M AME; *Darién*, Caña (1000m) 3F USNM; Cerro Piña 1M USNM. **VENEZUELA**: *Táchira*, Cucuta 1M BMNH; 1M, 2F AME; 2M USNM; No locality data 1M, 1F BMNH. **COLOMBIA**: *Chocó*, San Pablo, Río San Juan 1M BMNH; 2M ZMHU; *Caldas*, Cerro Aguacatal (1600m) 2M JHKW; *Boyacá*, Muzo 1F BMNH; *Valle del Cauca*, Calima Valley 1F AMNH; Juntas 1F BMNH; *Cauca*, Pescador (1450m) 1M AME. **ECUADOR**: *Imbabura,* Paramba 2F BMNH; *Pichincha,* Río Tanti (May, Jun) 2M, 2F JHKW; Tinalandia (Jul) 1F FSCA; Nanegal (1400m) 1F AME; *Los Ríos,* Río Palenque 1M, 1F AME; *Bolívar,* Balzapamba 1F AMNH; *Pastaza,* 9 km S. of Shell (Sept) 1M DA; 32 km S. of Puyo (Oct) 1M, 2F RCB; 1M GWB; *Napo,* km 4 Misahualli-Puerto Napo rd. (Oct) 2M, 1F RCB; Puerto Napo (Oct) 1M RCB; 1F GWB; Finca San Carlo (Feb, Sept) 5M JHKW; Cotundo 1M, 1F USNM; No locality data 1F MCZ. **PERU**: *Cuzco*, Paucartambo 1M MNHN. **BRAZIL**: *Rondônia*, environs of Fazenda Rancho Grande, nr. Cacaulândia 1M NSM; *Pará*, Rio Tapajós 1F BMNH; Pará 1M ZMHU; Amazonas 1M BMNH; *Maranháo*, No specific locality 1M BMNH; *Mato Grosso*, Chapada 1F BMNH; Diamantino 3M USNM; *Rio de Janeiro*, No specific locality 1M BMNH; 1M MCZ; No locality data 1M, 1F BMNH. **GUYANA**: *Upper Takutu/Upper Essequibo*, Essequibo river 1F BMNH. **FRENCH GUIANA**: *Cayenne*, La Mara 1M MNHN; No locality data 2M, 1F BMNH. **TRINIDAD**: Port of Spain 1M, 1F BMNH; Tabaquite 1M BMNH; St. Annes 2M AME; Arima Valley 1M, 2F AMNH; Santa Cruz 1F AMNH; No locality data 1M, 2F AME; 1F MNHN; 2M, 1F AMNH. No locality data 1M, 1F BMNH.

Theope theritas Hewitson, 1860

Figs. 57a-d; 124; 192; 248; 271.

Theope theritas Hewitson, 1860. *Ill. exot. Butts.* 2: 97, pl. 49, figs. 2, 3. **TL**: Amazon. Syntype male BMNH [Examined].

Identification and Taxonomy: Average forewing length: male 17mm, female 18mm.

MALE: *T. theritas* is one of the more easily identified species of the "*theritas* group" both because it is the largest and it has two (and sometimes other fainter) black spots in the tornus of the VHW. The ventral ground color is also slightly paler than that of *T. sobrina* but darker than that of *T. thootes, T. apheles* and *T. nodosus*, and the blue on the DFW is more regularly triangular, with a straighter distal edge than in any other species. The "paddle"-shaped, left-hand, posterior projection from the vinculum of the male genitalia is also consistently broader than that of the most similar species *T. thootes*, and may be the best diagnostic character if the tornal parts of the hindwings are missing; the last tergite is also very large and has more of a rectangular projection from the lower posterior corner than other "*theritas* group" species.

FEMALE: again, the female of *T. theritas* is recognised by its large size, dark ventral ground color and the presence of two or more conspicuous black spots at the distal submargin of the VHW (these may have a hint of white scaling proximally). The amount of blue is somewhat variable on both dorsal wing surfaces and blue may or may not be present in cell Sc+R1 on the hindwing. The last abdominal tergite of *T. theritas* has an elongate sclerotised disc at the upper posterior corner that distinguishes it from all similar species except *T. thootes*. The lack of a prominent dorso-lateral flange on the ostium bursae of the female genitalia additionally separates it from *T. thootes* and also the equally similar *T. sobrina*.

Biology: Nothing is known with certainty about the biology of this rare species. Callaghan (1983) records *T. theritas* as hilltopping in Villavicencio, east Colombia, from 1315 to 1400h, but since I know of no specimens of this species from Colombia and it is quite possible to confuse it with other "*theritas* group" species, his identification must be treated as tentative.

Distribution: This species has a broad Amazonian range but the vast majority of specimens originate from the middle and lower Amazon. C. Brévignon (pers. comm.) reports finding this species in French Guiana.

Specimens Examined: 13M 7F

PERU: *Madre de Dios*, Parque Nacional del Manu, Pakitza 2M, 1F USNM; *Puno*, Chaquimayo 1F BMNH. **BRAZIL**: *Amazonas*, Tefé 1M AME; Manicoré 1M ZMHU; *Rondônia*, environs of Fazenda Rancho Grande, nr. Cacaulândia 1M NSM; *Pará*, Rio Tapajós 1M, 1F BMNH; Itaituba 1M ZMHU; Santarem 1F ZMHU; 1F MNHN; Pará 1M, 1F BMNH; Amazon 1M BMNH; 1M MNHN. **GUYANA**: *Potaro/Siparuni*, Potaro river 1F AME. No locality data 1M BMNH; 1M USNM; 1M MNHN.

Theope thootes Hewitson, 1860

Figs. 58a-d; 125; 193; 249; 271.

Theope thootes Hewitson, 1860. *Ill. Exot. Butts.* 2: 98, pl. 49, figs. 9, 10. **TL**: Pará, E. Brazil. Syntype female BMNH [Examined].

Identification and Taxonomy: Average forewing length: both sexes 15mm.

MALE: although *T. thootes* was described from a female specimen, males that are of the same size and that have a similar wing shape and ventral ground color can be matched to the syntype with confidence. They are notable only for having no uniquely distinguishing features and the species is therefore rather difficult to identify. Males are larger than those of *T. apheles* and *T. nodosus* and have a darker ventral surface, although it is not as dark as that of the similarly sized males of *T. sobrina*, with which they are most often confused in museum collections. Based on wing pattern, *T. thootes* is most readily distinguished from *T. sobrina* by having a less prominent area of pale brown scales at the base of the DHW that barely intrudes into the discal cell. The male genitalia of *T. thootes* place it closest to *T. apheles*, and only differ by typically having a slightly broader left-hand, posterior projection from the vinculum.

FEMALE: female *T. thootes* is perhaps most similar to female *T. sobrina*, but its hindwing is more rounded and not as narrow, its ventral surface is paler and always lacks submarginal black spots on the hindwing, and the blue of the DFW tends to be in a more pronounced sideways "U" shape, although the extent of anal, postdiscal and costal blue on the forewing is variable. It is slightly larger than the female of *T. apheles*, has a darker ventral surface, and has typically less blue in cells Cu1 and M3 of the DFW. The last abdominal tergite of female *T. thootes* has a posteriorly elongate sclerotised disc at the upper posterior corner, a character shared only with *T. theritas*. This is a definitive character to distinguish *T. thootes* from the females of the two most similar species, *T. apheles* and *T. sobrina*, and one that can be examined under a microscope without dissection of the specimen, by rubbing scales from the abdominal tip.

Biology: Nothing is known about the biology of this uncommon to rare species.

Distribution: *T. thootes* is known to occur in the Guianas and throughout much of the Amazon basin, as far west as Iquitos, Peru, but it will probably eventually be found as far west as the base of the Andes. Kaye (1904, 1921) and Barcant (1970) report *T. thootes* from Trinidad, but these records are based on misidentifications of *T. phaeo* (see Appendix A), and a specimen in the BMNH from Nicaragua, mentioned by Godman and Salvin (1886), is certainly mislabelled.

Specimens Examined: 20M 16F

PERU: *Loreto*, Iquitos 2M MNHN; 1F USNM; 1F ZMHU. **BRAZIL**: *Amazonas*, Ipiranga 2M MNHN; *Rondônia*, environs of Fazenda Rancho Grande, nr. Cacaulândia 4M, 1F NSM; *Pará*, 1M Rio Tapajós BMNH; Pará 5M, 7F BMNH; Amazon 1M BMNH; No locality data 1F BMNH. **FRENCH GUIANA**: *Cayenne*, Cayenne 1M, 3F BMNH; Galion 1M USNM; No locality data 1M, 2F BMNH. Mislabelled: Nicaragua 1M BMNH. No locality data 1M BMNH.

Theope apheles Bates, 1868

Figs. 59a-d; 126; 194; 250; 271.

Theope apheles Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 405. **TL**: Ega, W. Brazil. Syntype male and female BMNH [Examined]; Lectotype male BMNH [Designated].

Identification and Taxonomy: Average forewing length: both sexes 12.5mm.

MALE: the male genitalia of *T. apheles* are very similar to those of *T. thootes* but the species can be distinguished from *T. thootes* and all others in the "*theritas* group" by its relatively small size, pale gray-brown ventral surface and characteristically convex distal forewing margin. Pale brown scales intrude slightly into the discal cell of the DHW as they do in *T. thootes*, but these are absent from *T. nodosus*. The male type of *T. apheles* has a conspicuously concave distal edge to the blue of the DFW, as is found in *T. nodosus*, but this specimen appears to be atypical in this regard, and all other characters, including the male genitalia, prove that the type is conspecific with the more typical specimen illustrated here.

FEMALE: the small female of *T. apheles* has more extensive and paler dorsal blue than its closest relatives and has a dorsal surface most similar to that of female *T. zostera*, although this species has a quite different ventral surface. The as yet unknown female of *T. nodosus* will undoubtedly be superficially very similar to that of *T. apheles*, and this should be borne in mind if any variation is observed among a sympatric series of putative *T. apheles* females. However, given that the male genitalia of the two species place them in different subsets of the "*theritas* group", the female genitalia are also very likely to differ significantly and thus provide the best characters for identification. The small sclerotised disc at the upper posterior margin of the last tergite in *T. apheles* is not elongate as it is in the most similar known female, that of *T. thootes.*

Due to the uncertainty in identifying female *T. apheles*, with respect to the as yet unknown or at least unrecognised female of *T. nodosus*, it seems prudent to designate the male syntype of *T. apheles* as a lectotype. This specimen in the BMNH bears the following labels: "apheles", "Theope/apheles,/Bates./Godman-Salvin/Coll. 1914.-5.", "Ega,/U. Amazons./H.W. Bates", "Type, H.T.".

Biology: This species is uncommon to rare in intact rainforest habitats below 600m. In Ecuador, I encountered solitary males perching about 2 to 4 meters above the ground in shaded hilltop lightgaps from 1100 to 1415h.

Distribution: *T. apheles* ranges widely from the base of the eastern Andes to the Guianas but the majority of specimens have been collected in the western Amazon. I regard a historical ZMHU specimen from Rio de Janeiro in south-east Brazil as a mislabelling, given the great distance of this locality from the nearest modern *bona fide* records. The following additional locality is reported to me by J.-Y. Gallard (pers. comm.) from BOLIVIA: *Santa Cruz*, Buena Vista.

Specimens Examined: 13M 7F

ECUADOR: *Sucumbíos,* Garzacocha, La Selva 1M PJD; *Napo*, Chichicorrumi (Feb) 2M JHKW; km 4 Tena-Pano rd. (Sept) 1F DA; Finca San Carlo (Feb, Sept) 2M JHKW; Pimpilala (Feb) 1F JHKW; *Morona-Santiago*, Taisha (Jun) 1M JHKW. **PERU**: *Loreto*, Iquitos 1F BMNH; *Madre de Dios*, Boca Río La Torre 1M USNM; *Puno*, La Union, Río Huacamayo, Carabaya 1F BMNH. **BRAZIL**: *Amazonas*, Ega 1M, 1F BMNH. **FRENCH GUIANA**: *Cayenne*, Galion 4M, 2F USNM. Mislabelled: Rio de Janeiro, Brazil 1M ZMHU.

Theope sobrina Bates, 1868

Figs. 3d-e, m-o; 54a-d; 122; 189; 247; 270.

Theope sobrina Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 405. **TL**: Rio Tapajós, E. Brazil. Syntype female BMNH [Examined].

Identification and Taxonomy: Average forewing length: male 14.5mm, female 13.5mm.

MALE: although this species was described from a single female specimen, the male can be matched to the female syntype with some certainty as I have examined two pairs that were caught *in copulo* in French Guiana and Ecuador (J.-Y. Gallard, pers. comm.; pers. obs.). It is figured here as the male of *T. sobrina* for the first time. Three wing pattern characters best diagnose male *T. sobrina*: its broad wing shape, with a narrowly angular hindwing, its dark ventral ground color, and the presence of a prominent ovoid area of pale brown scales near the base of the DHW that protrudes extensively into the discal cell. The dorsal blue is also often darker than that of other species in the group and *T. sobrina*, like *T. thootes,* only has blue in the basal half of the upper portion of the discal cell of the DFW, with dark brown scales occurring in the more distal half and postdiscally (most visible in fresh specimens). The genitalia of *T. sobrina*, unusually for the "*theritas* group", are largely symmetrical and utterly distinctive, with a unique combination of pairs of spiked projections on the vinculum, valvae and last sternite; unlike all species in the group except *T. zostera*, *T. sobrina* also lacks a large projection from the lower posterior corner of the last tergite.

FEMALE: female *T. sobrina* can often be difficult to separate from female *T. thootes* based on wing pattern characters, but, like the male, it has a broader wing shape, with a similarly narrow and rather angular hindwing, and a darker ventral surface, although this is variable and in specimens with a ventral ground color intermediate between that of typical *T. thootes* and typical *T. sobrina*, the variable presence of two or more tiny black spots in the tornus of the VHW can aid identification. Since female *T. sobrina* is rather variable in size, the exact hue of the ventral surface, and in the amount of blue postdiscally on the DFW and at the costa of the DHW, the genitalia may need to be examined to make a definitive identification. Having examined the genitalia of the female syntypes of *T. sobrina* and *T. thootes*, and several other specimens, including one of the aforementioned females of *T. sobrina* collected *in copulo*, it is evident that the shape of the last tergite most easily allows separation; both species have a last tergite that has a sclerotised disc in the upper posterior corner, but in *T. thootes* this is markedly posteriorly elongate to form an inverted "L"-shaped tergite. The ostium bursae of the female genitalia of *T. sobrina* also has more prominent dorso-lateral projections than that of *T. thootes*.

Biology: Although *T. sobrina* has rarely been recognised as a valid species in collections and the literature, due to uncertainty as to whether the female syntype represented only a mere form of *T. thootes*, it is actually the most commonly represented "*theritas* group" species in collections after *T. phaeo*. It occurs locally in lowland rainforest habitats up to 600m. In Ecuador, I encountered solitary males perching 1 to 3 meters above the ground at the shaded edge of hilltop lightgaps between 1200 and 1330h. A pair was found *in copulo* in such a site at 12 mid-day, at the very beginning of the male perching period.

Distribution: *T. sobrina* occurs throughout the Guianan and Amazon regions, extending as far south as Goiás state in south Brazil.

Specimens Examined: 70M 40F

VENEZUELA: *Bolívar*, Suapure 3M MCZ; *Amazonas*, Cerro de la Neblina 1F USNM. **COLOMBIA**: *Caquetá*, Montañita 1M USNM; *Cundinamarca*, Medina 1M MNHN. **ECUADOR**: *Napo,* Chichicorrumi 2M (Jul, Dec) JHKW; km 4 Tena-Pano rd. (Sept) 1M DA; Apuya (Feb, Oct) 1F JHKW; 1M GWB; Finca San Carlo (Sept, Dec) 2M, 1F JHKW; Río Napo 1M BMNH; No locality data 1M BMNH. **PERU**: *Loreto*, Iquitos 4M, 7F MNHN; Balsapuerto 1M MNHN; Río Nanay 1F MNHN; Pebas 1F ZMHU; *San Martín*, Juanjuí 3M MNHN; Chazuta 1M MNHN; *Huánuco*, Río Pachitea 2M ZMHU; *Madre de Dios*, Parque Nacional del Manu, Pakitza 4M, 1F USNM; *Puno*, La Union, Río Huacamayo, Carabaya 1M, 1F BMNH. **BRAZIL:** *Amazonas*, Tabatinga 1M ZMHU; São Paulo de Olivença 1F MNHN; Ipiranga 2M, 1F MNHN; Humaitá 1M BMNH; Manicoré 2M ZMHU; Tomar 1F ZMHU; *Rondônia*, environs of Fazenda Rancho Grande, nr. Cacaulândia 2M NSM; *Pará*, Rio Tapajós 1M MNHN; Itaituba 1M, 1F ZMHU; Santarem 1F ZMHU; Pará 6F BMNH; 1F AME; Amazon 1F BMNH; *Maranháo*, No specific locality 1M BMNH; *Goiás*, Santa Rita do Araguaia 1M, 3F USNM; No locality data 1M BMNH. **GUYANA**: *Upper Takutu/Upper Essequibo*, Annai, Essequibo river 2M BMNH; *Potaro/Siparuni*, Tumatumari 1M AME; *Cuyuni/Mazaruni*, Carimang river 1M BMNH; *Demerara/Mahaica*, No specific locality 1M BMNH. **SURINAM**: No locality data 1M BMNH. **FRENCH GUIANA**: *Cayenne*, Cayenne 3M BMNH; Galion, Roura 12M, 5F USNM; 1M, 1F JHKW; Mts. des Chevaux 2M USNM; Route de L'est 1M USNM; No locality data 2M, 1F BMNH. No locality data 2M, 1F BMNH; 1F ZMHU; 1F MCZ.

GROUP XIII: "*thestias* group"

Theope janus Bates, 1867

Figs. 60a-f; 127; 195; 251; 272.

Theope janus Bates, 1867. *Trans. ent. Soc. Lond.* (3)5(7): 546. **TL**: Montes Aureos, E. Brazil. Syntype male BMNH [Examined].

Identification and Taxonomy: Average forewing length: both sexes 11mm.

MALE: *T. janus* is the most distinctive species in the "*thestias* group", due to the wide yellow band that occupies the basal third of both ventral wing surfaces and the yellow tipped abdomen. The male genitalia of *T. janus* are most like those of *T. guillaumei*, in having a small uncus, straight vinculum and evenly sized aedeagus, although the male genitalia of all species in the group exhibit only minor variation; an exceptional genitalic autapomorphy for *T. janus* is the possession of an anteriorly bifid, "hammer"-shaped subscaphium. Characters such as the lack of ventral purple iridescence, which is shared only with *T. guillaumei* in this group, and the possession of a contorted anterior portion to the aedeagus, which is shared with "*theritas*" and "*foliorum* group" species, place *T. janus* at the base of the "*thestias* group" (Hall, in prep.). Typically, the blue on the DFW of *T. janus* extends in a narrow apically directed triangle but in the single west Amazonian specimen examined, this blue is restricted to the very base of the anal margin and there is also some sparse blue scaling beneath the discal cell of the DHW. The wing shape of this specimen is also more compact and pointed, but the male genitalia do not differ from typical specimens.

FEMALE: the strongly dimorphic female is diagnosed by the same characters given above for the male, but additionally has a most unusual dorsal surface, with blue restricted to the upper half of the hindwing and appearing as distal rays on the forewing.

Biology: Nothing is known about the biology of this rare species.

Distribution: *T. janus* occurs in the Guianas and along much of the length of the Amazon river system. Museum specimens predominantly originate from the lower Amazon, but the single MNHN record from Iquitos, Peru, suggests that it may range more widely in the upper Amazon region.

Specimens Examined: 8M 2F

PERU: *Loreto*, Iquitos 1M MNHN. **BRAZIL**: *Pará*, Pará 2M, 1F BMNH; *Maranhão*, Montes Aureos 3M, 1F BMNH. **FRENCH GUIANA**: *Cayenne*, Galion (Jan) 1M USNM. No locality data 1M ZMHU.

Theope guillaumei Gallard, 1996

Theope guillaumei guillaumei Gallard, 1996

Figs. 61a,b; 252; 272.

Theope guillaumei Gallard, 1996. *Lambillionea* 100: 43-46, figs. 1-4. **TL**: Crique Toussaint, Sinnamary, French Guiana. Holotype male and allotype female in coll. J.-Y. Gallard, French Guiana; type illustrations [Examined].

Identification and Taxonomy: Average forewing length: male 9mm, female 9.5mm.

Sexes similar but female has more rounded wings and, in some specimens, traces of blue at the base of both dorsal wing surfaces. The nominate subspecies of *T. guillaumei* is readily distinguishable from other "*thestias* group" species by its small size, uniform brown ventral color, which has no traces of purple iridescence and only a small area of yellow at the base of the forewing, and most notably by its entirely (in males) or predominantly (in certain female specimens) brown dorsal surface. The forewing venation of *T. guillaumei* is notable for having veins Sc and R1 completely fused, a character shared only with the distantly related *T. orphana*.

Biology: *T. guillaumei* remained long undiscovered, but recently has almost simultaneously been collected by lepidopterists in several Neotropical localities. The nominate subspecies is widespread but clearly very rare and virtually nothing is known of its adult biology. In the original description, Gallard (1996) reports only that the solitary male holotype was captured resting beneath a leaf along a creek at 1000h and a single female was captured in the same vicinity two years later. R. Busby (pers. comm.) reports finding a male on a flowering bush at the forest edge.

Distribution: Nominate *T. guillaumei* is currently recorded from disparate localities in only three countries, at the base of the eastern Andes, in south-west Amazonia and the Guianas, but it should occur in all Amazonian and Guianan countries.

Specimens Examined: 1M 2F

ECUADOR: *Napo,* km 4 Misahualli-Puerto Napo rd. (Oct) 1M RCB. **BRAZIL**: *Rondônia*, environs of Fazenda Rancho Grande, nr. Cacaulândia (Nov) 2F NSM.

Theope guillaumei cecropia DeVries & Hall, 1996

Figs. 61c-f; 128; 196; 252; 272.

Theope guillaumei cecropia DeVries & Hall, 1996. *Trop. Lepid.* 7(1): 88-90, figs. 2a,b. **TL**: Finca La Selva, Costa Rica. Holotype female AMNH [Examined].

Identification and Taxonomy: Average forewing length: male 9mm, female 9.5mm.

This subspecies differs from the nominate only in the female, which has an entirely pale blue DHW, except for an uneven black distal margin, and a triangular area of pale blue at the base of the DFW below the discal cell. The female resembles that of *T. thestias*, but has a greatly reduced hindwing anal fold, paler blue dorsal coloration, no trace of ventral purple iridescence, and a smaller yellow area at the base of the VFW. The male genitalia of *T. guillaumei cecropia* differ only minorly from those of *T. thestias* in the smaller size of the uncus and the uniform thickness of the aedeagus, which does not curve sharply upwards at its distal end.

Biology: Incredibly, given the rarity of this species, the subspecies *cecropia* was discovered through the rearing of larvae and only a single adult has, to my knowledge, ever been seen in nature. The foodplant, *Cecropia insignis* (Cecropiaceae or Urticaceae [*sensu lato*]) was first reported by DeVries *et al.* (1994) under the name "*Theope* nr. *decorata*". The following life history details are quoted from the original description of *T. guillaumei cecropia* (DeVries and Hall, 1996): "The mature caterpillar has a gray body with a broad rich maroon dorsal mid-line that has the distal edges somewhat jagged and bordered by white; a conspicuous black dot on the posterior margin of all abdominal segments; anal plate with a distinct central black triangle with the apex directed toward posterior; areas distal to this triangle are pale pink; the areas surrounding the tentacle nectary organs are rich maroon; the head is brown surrounded by a sparse corona of short brown balloon-setae; the anterior edge of the first thoracic segment, the interface of all abdominal segments, and the venter with fairly long white setae.

The caterpillars were semi-gregarious and skeletonized the underside of a single *C. insignis* leaf near the radiating central veins. These caterpillars were not tended by the *Azteca* (Dolichoderinae) ants that inhabited the *Cecropia* tree, but rather by the *Solenopsis* (Myrmicinae - *Diplorhoptrum* group) ants that formed small colonies in the radiating leaf veins at the base of the petiole. The caterpillars were never observed interacting with the *Azteca* ants. The caterpillars were loosely gregarious when resting near the radiating central veins of the leaf, and less so when feeding. The caterpillars possess vibratory papillae, and produce a call like other members of the riodinid tribe Nymphidiini (DeVries, 1990, 1991). Pupation took place in a curled edge of the hostplant leaf, and the pupa resembles a tiny version of other members of *Theope*". An illustration of the mature larva is given in both DeVries and Hall (1996) and DeVries (1997). It is interesting to note the female-biased sex ratio of 6:1 in the resulting adults from the small aforementioned colony of larvae.

Distribution: This subspecies is currently only known from Costa Rica. Surprisingly, no specimens were ever collected by the late G. B. Small and H. L. King in neighbouring Panama, despite intensive collecting effort; it must occur there as well as in the west Andean region of Colombia and probably Ecuador.

Specimens Examined: 2M 6F

COSTA RICA: *Heredia*, Finca La Selva (Feb, Mar) 1M, 5F AMNH; 1F MNCR; *Limón*, Río Blanco-Petroleo rd., Río Victoria (Apr) 1M USNM.

Theope discus Bates, 1868

Figs. 62a-d; 129; 197; 253; 272.

Theope discus Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 409. **TL**: Pará, E. Brazil. Syntype male BMNH [Examined]; Lectotype male BMNH [Designated]. **[stat. rev.]**

Identification and Taxonomy: Average forewing length: both sexes 11mm.

MALE: *T. discus* was described as a full species by Bates (1868), but subsequently treated as a form of *T. thestias* by Stichel (1911, 1930), Seitz (1920) and thus Bridges (1994). However, its broad sympatry with *T. thestias* and the wing pattern differences outlined below clearly establish it as a distinct species. It differs from *T. thestias* by having a pale brown instead of dark brown dorsal ground color (especially in lower Amazonian populations and in comparison with sympatric Amazonian populations of *T. thestias*), reduced, paler blue on both dorsal wing surfaces that is almost absent from the upper half of the discal cells and has a jagged, almost rayed distal edge on the hindwing with the veins weakly outlined in brown, and typically a slightly narrower and more smoothly curving area of pale purple at the base of the VFW, with a broader area of dark brown distally. It is readily distinguished from *T. decorata* by having a paler dorsal ground color, reduced blue on the DHW and a solid, irregular triangle of blue on the DFW. Both sexes of *T. discus* from the western Amazon have slightly more blue on the DHW.

FEMALE: the female has the same ventral and dorsal characteristics of the male, although the blue is slightly more extensive on the dorsal surface, forming a small semicircle on the forewing and often a more rounded area on the hindwing (at least in west Amazonian specimens). It is additionally distinguished from the females of similar "*thestias* group" species by having an exaggeratedly rounded wing shape and, most importantly, by exhibiting sexual monomorphism in the shape and hue of the yellow region at the base of the VFW, which is not enlarged, nor a purer paler yellow, as it is in *T. thestias* and *T. decorata*.

Since there are no males of *T. discus* in the BMNH from the upper Amazon, one of the original type localities, there is the possibility of a mixed type series for this species. I therefore designate the only labelled syntype in the BMNH, from the remaining type locality, a lectotype, a specimen which bears the following labels: "discus", "Theope/discus,/Bates./Godman-Salvin/Coll. 1914.-5.", "Para,/L. Amazons./H.W. Bates", "Type, H.T.".

Biology: *T. discus* is the rarest in the trio of "*thestias* group" sibling species, and little is known of its biology. In Ecuador, a female was found in a rotting fish-baited trap placed 5 meters above the ground in a forest lightgap at 1450h.

Distribution: The majority of museum specimens originate from the Guianas and lower Amazon, but recent collecting efforts have uncovered the species at several sites along the base of the eastern Andes.

Specimens Examined: 10M 5F

COLOMBIA: No locality data 1F JS. **ECUADOR**: *Sucumbíos,* Garzacocha, La Selva 1M PJD; *Napo,* Laguna de Pañacocha (Oct) 1F JHKW; Limoncocha 1F USNM; km 4 Misahualli-Puerto Napo rd. (Oct) 1F RCB; Jatun Sacha (Oct) 1M DA; Cotundo 1M AME. **PERU**: *Loreto*, Iquitos 1F BMNH; *Madre de Dios*, Parque Nacional del Manu, Pakitza 1M, 1F USNM. **BRAZIL**: *Pará*, Pará 4M BMNH. **FRENCH GUIANA**: *Cayenne*, Cayenne 1M BMNH; *Saint Laurent du Maroni*, Saint Laurent du Maroni 1M BMNH.

Theope thestias Hewitson, 1860

Figs. 63a-f; 130; 198; 254; 272.

Theope thestias Hewitson, 1860. *Ill. Exot. Butts.* 2: 98, pl. 49, figs. 5, 6. **TL**: Not Stated. Syntype female BMNH [Examined].

Identification and Taxonomy: Average forewing length: both sexes 11mm.

MALE: *T. thestias* is very similar to *T. decorata* and *T. discus*, which until this work have almost universally been regarded as forms or subspecies of *T. thestias* (Stichel, 1911, 1930; Seitz, 1920; Bridges, 1994). *T. thestias* differs from *T. decorata* by having a solid triangle of blue on the DFW, often more blue on the DHW with a more jagged distal edge, and typically less yellow at the base of the VFW with a broader, more angular area of pale purple distally. It differs from *T. discus* by having a dark brown instead of pale brown dorsal ground color (at least in sympatric Amazonian specimens), increased, darker blue on both dorsal wing surfaces that forms more of an apically directed triangle on the forewing than an irregular semicircle, and again, typically a more angular area of pale purple on the VFW that creates a narrower medial band of dark brown which may also be apparent on the VHW. This last character is most noticeable on specimens from the southern-most part of the range of *T. thestias*; these specimens also tend to have a paler ventral surface, a slightly paler dorsal ground color and paler dorsal blue that extends further along the anal margin of the hindwing. Throughout the Amazon basin, the amount of blue on the DFW is variable.

FEMALE: female *T. thestias* largely shares the same wing pattern characters of sympatric males, but the yellow at the base of the VFW is enlarged and of a paler, purer hue. This distinguishes it from *T. discus*, which is sexually monomorphic for this character, and Amazonian females of *T. decorata*, which have a larger, more angular, richer yellow region. All females of *T. decorata* may be distinguished on the dorsal surface by having blue rays along the anal margin and, especially in South American specimens, also through the discal cell, instead of having a solid triangle. In southerly populations of *T. thestias*, females share all those characters mentioned above for males, except that blue typically covers the entire DHW. Although the syntype female of *T. thestias* bears no locality data, it clearly originates from one of these southerly populations along the south-eastern seaboard of Brazil.

Biology: Although the most well represented "*thestias* group" species in collections, little is known of the biology of this species. It occurs in association with a variety of lowland forest habitats up to 1000m, and from label data and personal experience, it appears to be typically encountered in bright forest edge microhabitats and it is certainly tolerant of degraded forest. The conclusion of these somewhat anecdotal comments is supported by the fact that the foodplant for the closely related species *T. guillaumei*, is *Cecropia*, a predominantly secondary growth tree that may be an important foodplant for all "*thestias* group" species. In Ecuador, a solitary male was encountered perching 5 meters above the ground in a large streamside clearing towards the forest edge at 1300h, as part of a species-rich riodinid perching community. Brown (1992) reports finding this species on flowers.

Distribution: This is a widespread species that occurs in the Guianas, throughout the Amazon basin and as far south as Paraguay and Santa Caterina state in south-east Brazil. The majority of museum specimens originate from the southern portion of this range, where it appears to be more common. The following additional locality is listed by Brown (1992) (as *T. thestias discus* - but see Fig. 93 in that work) for BRAZIL: *São Paulo*, Serra do Japi.

Specimens Examined: 73M 60F

COLOMBIA: *Caquetá*, Río Bodoquero 1F USNM. **ECUADOR**: *Pastaza*, 25 km N. of Puyo (Oct) 1M, 1F GWB; *Napo*, km 4 Misahualli-Puerto Napo rd. (Oct) 2M RCB; Río Napo 1M BMNH; Pimpilala (Oct) 1M JHKW; No locality data 1F BMNH. **PERU**: *Loreto*, Iquitos 1M BMNH; 1M, 1F ZMHU; 3M, 1F MNHN; Yurimaguas 1F ZMHU; *Huánuco*, 1 km S. of Las Pampas 1F AME; *Junín*, No specific locality 1M BMNH; *Madre de Dios*, Parque Nacional del Manu, Pakitza 5M USNM; No specific locality 1F MNHN; *Cuzco*, Marcapata 1M ZMHU; 1F MNHN; San Pedro (1400m) 1F USNM; No locality data 1F MNHN. **BOLIVIA**: *La Paz*, Mapiri 1M, 1F ZMHU; Coroico 1F BMNH; Río Songo 1F BMNH; 1F ZMHU; No specific locality 1M ZMHU. **BRAZIL**: *Amazonas*, São Paulo de Olivença 1F MNHN; Tonantins 2M BMNH; Humaitá 2M BMNH; Tomar 1M ZMHU; *Rondônia*, environs of Fazenda Rancho Grande, nr. Cacaulândia 5M NSM; *Pará*, Pará 1M BMNH; 1M ZMHU; *Espírito Santo*, No specific locality 1F BMNH; *Distrito Federal*, Parque do Gama 1F USNM; *Minas Gerais*, 1F Leopoldina ZMHU; No specific locality 1F BMNH; 1M MNHN; *São Paulo*, São Paulo 2F BMNH; *Paraná*, Fernández Pinheiro (2600ft) 1M, 3F BMNH; 1M AME; Iguaçu 2M, 2F BMNH; 1M, 1F MNHN; União da Vitória (2000ft) 1M BMNH; 30 km N.W. of Ponta Grossa 3F USNM; Castro 2F BMNH; *Santa Catarina*, Joinvile 1M, 3F AME; Rio Lacisz 2M, 1F AMNH; Annaburg 2M, 1F AMNH; Nova Teutonia 1M USNM; No specific locality 1F BMNH; 1M ZMHU; 1F USNM; 4M AMNH; 2F MCZ; *Rio Grande do Sul*, Pelotas 1F AME; 2M, 4F MCZ; No specific locality 1M BMNH; 1M, 3F ZMHU; 2F MNHN; No locality data 1F BMNH; 2M, 1F ZMHU. **PARAGUAY**: *Caaguazu*, San José 1F BMNH; *Alto Paraná*, Puerto Bertoni 1F ZMHU; *Itapúa*, Hohenau 1F MNHN; ? S. Paraguay 2F BMNH. **FRENCH GUIANA**: *Cayenne*, Cayenne 5M BMNH; *Saint Laurent du Maroni*, Saint Laurent du Maroni 2M MNHN; No locality data 5M BMNH;

1M MNHN. ? San Juan de la Sello 1M ZMHU. No locality data 2M, 1F BMNH; 2M ZMHU.

Theope decorata Godman & Salvin, 1878

Figs. 2c, j-k; 64a-h; 131; 199; 255; 272.

Theope decorata Godman & Salvin, 1878. *Proc. zool. Soc. Lond.* 1878(2): 369. **TL**: Chontales, Nicaragua. Syntype female (described as a male) BMNH [Examined]. **[stat. rev.]**

Identification and Taxonomy: Average forewing length: both sexes 11mm.

MALE: *T. decorata* was described as a full species by Godman and Salvin (1878), but subsequently treated as a subspecies of *T. thestias* by Stichel (1911, 1930), Seitz (1920), Bridges (1994) and DeVries (1997). However, its partial sympatry with *T. thestias* and the wing pattern differences outlined below clearly establish it as a distinct species. *T. decorata* consistently differs from *T. thestias* and *T. discus* by having greatly reduced blue on the DFW that is restricted to the anal margin and in some specimens a ray through the discal cell, a smoother distal edge to the blue of the DHW and typically a narrower, brighter purple arc on the VFW that leaves a broader dark brown medial area. There are no significant differences in the male genitalia of the three species. Males of *T. decorata* are variable in the amount of dorsal blue, especially on the forewing, where it may consist of a prominent bar along the anal margin and/or through the discal cell or be practically absent, the amount of black scaling in the discal cell of the DHW, and in the extent and hue of the yellow at the base of the VFW; in coloration it may be a dirty greenish-yellow or a purer yellow as in the female.

FEMALE: female *T. decorata* may be readily distinguished from similar species by the characters outlined above for the male. It is similarly variable, but this variation is correlated with geographic location. Compared to nominotypical Central American specimens, those provisionally identified here as belonging to *T. decorata* from the Guianas and Amazon basin have a more prominent blue ray through the discal cell of the DFW, often with further rays postdiscally, a variably broad black distal margin on the DHW, purple postdiscal iridescence on the VHW and, most notably, a broader, rectangular, richer yellow region at the base of the VFW. They may represent a distinct taxon, but without any matching males from the Amazon basin (see discussion below about sex ratios) and specimens of either sex from intermediate areas of northern South America, there is presently not enough information to make any firm conclusions.

Biology: Little is known about the biology of *T. decorata*. In western Ecuador, a solitary male was encountered perching on top of a leaf about 2 meters above the ground along the edge of a very broad ridgetop path at 1330h and thus both in flight and at rest looked very much like a lycaenid. Although the females of most *Theope* species are more poorly represented in collections than males, *T. decorata* is extraordinary in having an almost 1:5 male:female ratio amongst examined specimens. This might be explained by the fact that females are more easily observed and collected, because of factors such as they fly closer to the ground, in more open and easily accessible microhabitats or are active for longer periods of the day. However, even amongst reared adults of the closely related *T. guillaumei* a similar 1:6 ratio was found, suggesting that a female-biased sex ratio might actually be a genuine phenomenon in the "*thestias* group" (see introductory "Biology" section).

Distribution: *T. decorata* ranges from Nicaragua to western Ecuador, and occurs in the Guianas and the central, lower and southern portions of the Amazon basin, no specimens being known from the base of the eastern Andes. The following additional locality is listed by DeVries (1997) for COSTA RICA: *Cartago*, Turrialba.

Specimens Examined: 11M 47F

NICARAGUA: *Atlántico Sur*, Rama 1M AME; *Chontales*, No specific locality 1F BMNH; No locality data 1F BMNH. **COSTA RICA**: *Puntarenas*, Llorona 1F USNM; Sirena 2F PJD. **PANAMA**: *Chiriquí*, Bugaba 2M ZMHU; 1M USNM; Lino 1M, 1F MNHN; No specific locality 1M MCZ; *Panamá*, El Llano 6F USNM; No specific locality 1F BMNH; 3M, 1F ZMHU; 1M, 1F MNHN; No locality data 1M, 1F MNHN. **COLOMBIA**: *Chocó*, Río San Juan 1F BMNH; 2F ZMHU; *Cundinamarca*, Bogotá 1F BMNH. **ECUADOR**: *Esmeraldas*, El Encanto, Lita-San Lorenzo rd. (Sept) 1F RCB; *Carchi*, nr. Lita, ridge to E. of Río Baboso (Jul) 1M JHKW. **BRAZIL**: *Amazonas*, São Paulo de Olivença 1F BMNH; Tonantins 1F BMNH; Manicoré 1F ZMHU; Amazon 1F BMNH; *Rondônia*, environs of Fazenda Rancho Grande, nr. Cacaulândia 5F NSM; *Mato Grosso*, Chapada 1F BMNH; 1F USNM; Cuiabá 1F BMNH; River system Cuiabá-Corumbá 1F BMNH; No specific locality 1F BMNH. **FRENCH GUIANA**: *Cayenne*, Cayenne 2F BMNH; No locality data 9F BMNH. No locality data 1F BMNH.

GROUP XIV: "*foliorum* group"

Theope lycaenina Bates, 1868

Figs. 2l-n; 3f,g; 65a-d; 132; 200; 256; 273.

Theope lycaenina Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 406. **TL**: Pará, E. Brazil. Syntype male and female BMNH [Examined]; Lectotype male BMNH [Designated].

Identification and Taxonomy: Average forewing length: both sexes 13.5mm.

MALE: *T. lycaenina* closely resembles many "*foliorum* group" species but is most often confused in collections with *T. methemona*, *T. sticheli* and *T. wallacei*. It differs from both by being smaller, having a more rounded forewing, a less robust thorax and abdomen, less prominent submarginal spots on the ventral surface that are typically restricted to the hindwing tornus, and more grainy dorsal blue coloration that is more extensive on both wings, always extending postdiscally into a rayed pattern on the forewing and extending further towards the distal margin of the hindwing. The prominence of ventral submarginal spotting in *T. lycaenina* is variable. Typical specimens have only a few spots in the hindwing tornus and may also be confused with *T. foliorum*, but this species has a more pointed forewing and never has any postdiscal blue on the DFW. Specimens in which these spots are barely discernible may resemble the distantly related *T. hypoleuca*, but *T. lycaenina* is larger, has a slightly darker ventral surface, more elongate wing shape, and darker dorsal blue that extends further towards the distal margin of the forewing and is more ray-like. The male genitalia of *T. lycaenina* are among the most distinctive of all the "*foliorum* group" species in having only a very small upper "arm" to the valvae, an unusually long triangular projection from the lower posterior corner of the uncus, and a relatively short aedeagus that opens to the right instead of upwards. These characters, among others, place *T. lycaenina* at the base of the entire "*foliorum* group" (Hall, in prep.).

FEMALE: females often have spots around the entire submargins of both ventral wing surfaces and therefore closely resemble the females of *T. wallacei* and *T. foliorum*; they differ from the former by their smaller size, more rounded wing shape, reduced blue on the DHW and more ray-like blue on the DFW, and from the latter by having darker dorsal blue that extends in a ray-like postdiscal pattern on the DFW, as in the male, and by having less prominent dark brown submarginal spots on the DHW. The female genitalia of *T. lycaenina* are notable for having the most exaggeratedly coiled posterior section to the ductus bursae of all the known "*foliorum* group" females.

Since both labelled syntypes originate from Pará and there is thus uncertainty concerning the specific identification of further unlabelled syntypes from the other original type locality, Santarem, I designate a male syntype in the BMNH as lectotype. It bears the following labels: "lycaenina/Bates", "Theope/lycaenina,/Bates./Godman-Salvin/Coll. 1914.-5.", "Para,/L. Amazons./H.W. Bates", "Type of/Theope/lycaenina/Bates.", "Type, H.T.".

Biology: *T. lycaenina* is one of the most commonly encountered *Theope* species in lowland Amazonia, where it occurs in wet forest habitats up to 1000m. Males are usually encountered perching in small groups on relatively low vegetation in lightgaps and along sunny forest trails, especially on ridgetops, from 1230 to 1500h. Of course, as their name suggests, in flight they look very much like lycaenids and they land both beneath and on top of leaves; in the latter case, K. Willmott (pers. comm.) informs me of observing them curiously resting facing the leaf stem instead of outwards. DeVries (1997) frequently observed females fluttering around new shoots of the hostplant which were growing near large colonies of *Azteca* ants.

An examination of reared voucher material indicates that the foodplants *Maripa panamensis* (Convulvulaceae) and *Gustavia superba* (Lecythidaceae), reported for "*Theope* nr. *thestias*" from Panama by DeVries *et al.* (1994), actually refer to *T. lycaenina*. The eggs are laid singly in the presence of *Azteca* ants (DeVries *et al.*, 1994). The mature caterpillar has a shiny black head capsule with a medial inverted white "V" shape, and a dense corona of dark purple, black and a few posterior white balloon setae on the prothoracic shield; the body has a broad green dorsal band bordered laterally by mottled bands of reddish, purplish and white spots, which have several white dots at the posterior margins of each abdominal segment, then another pale green band containing a long white latitudinal stripe, short tufts of sparse white lateral setae and an anal plate that is transparent except for a medial black band (DeVries, 1997). The solitary caterpillars feed on leaves and flower parts and are constantly tended by *Azteca* ants (DeVries *et al.*, 1994). The pale green pupa is typically folded inside a leaf of the hostplant or even covered with a thin layer of carton constructed by the *Azteca* ants (DeVries, 1997).

Distribution: This species is widespread throughout the Amazon and Guianan regions and its presence in Panama suggests that it also inhabits the intervening areas of the Chocó and northern Venezuela. The following additional localities are listed by DeVries (1997) for COSTA RICA: *Puntarenas*, Sirena; by Lamas *et al.* (1991) for PERU: *Loreto*, Castaña; and by Mielke & Casagrande ([1992]) for BRAZIL: *Roraima*, Ilha de Maracá.

Specimens Examined: 165M 77F

PANAMA: *Panamá*, Río Trinidad 2M USNM; *Canal Zone*, Summit 1M, 1F AME; Piña 1M, 1F FSCA; 2M, 2F AME; 2M USNM; Barro Colorado Is. 1M USNM; Cocoli 1M, 2F USNM; Madden Forest 2F USNM; Gatun 1M, 3F USNM; 1M DA; Gamboa 1M, 1F AME. **VENEZUELA**: *Bolívar*, Suapure 1M MCZ. **ECUADOR**: *Pastaza,* 25 km N. of Puyo (Oct, Feb) 2M GWB; 6M RCB; 32 km S. of Puyo (Oct) 1M GWB; 1M RCB; *Napo,* Río Tiputini (Mar, Apr) 2M JHKW; km 4 Misahualli-Puerto Napo rd. (Oct) 1M GWB; Jatun Sacha (Sept) 1M DA; Chichicorrumi (Feb, Sept) 2M JHKW; Tena 2M AME; Finca San Carlo (Apr) 1M JHKW; Apuya (Feb) 2M JHKW; Río Llandia (Dec) 1M JHKW; No locality data 1M BMNH. **PERU**: *Loreto*, Iquitos 6M MNHN; *San Martín*, Juanjuí 4M MNHN; *Huánuco*, Río Pachitea 2M, 1F ZMHU; *Madre de Dios*, Erika 2M, 1F USNM; 20 km S.W. of Puerto Maldonado 2M, 1F USNM; 10 km N. of Puerto Maldonado 3F USNM; Parque Nacional del Manu, Pakitza 4M USNM. **BRAZIL**:

Amazonas, Maués 2M ZMHU; 1M MNHN; Ipiranga 3M MNHN; Manaus 1F ZMHU; *Rondônia*, environs of Fazenda Rancho Grande, nr. Cacaulândia 8M, 2F NSM; *Pará*, Obidos 1M ZMHU; 3F ZMHU; Rio Tapajós 1F BMNH; Santarem 1F BMNH; Cuiabá-Santarem highway 1M USNM; Pará 9M, 4F BMNH; 1M, 3F ZMHU; Igarapé-Açu 3M, 1F AME; 5M, 3F AMNH; Amazon 1M, 1F BMNH; Rio Arapiuns 1M AME; *Mato Grosso*, Diamantino 1M USNM; *Distrito Federal*, Brasília 1F ZMHU; *Espírito Santo*, Linhares 12M, 17F AME; Conceiçao da Barra 1F USNM; *Rio de Janeiro*, Poco dos Antas 1M USNM; Rio de Janeiro 2M BMNH; No specific locality 2M BMNH; No locality data 2M BMNH. **GUYANA**: *East Berbice/Courantyne*, Camp Jaguar, New River Triangle 1M AME; *Upper Takutu/Upper Essequibo*, Annai, Essequibo river 6M, 1F BMNH; *Cuyuni/Mazaruni*, Carimang river 1M BMNH; No locality data 1M AMNH. **SURINAM**: *Paramaribo*, Paramaribo 1M BMNH. **FRENCH GUIANA**: *Cayenne*, Cayenne 2M BMNH; 1M USNM; Ríviere Kourou 4M BMNH; Vidal 2M, 3F USNM; Matoury 1M USNM; No locality data 1M BMNH; 1F USNM. **TRINIDAD**: St. Annes 3M BMNH; 2M MNHN; Maracas Falls 1M BMNH; 1F AMNH; 6 mi. N.W. of Arima 1M AME; 1M AMNH; Port of Spain 1M AME; Tabaquita 1M AMNH; Cascada Mt. rd. 1F AMNH; La Gloria Est., Gran Couva 1F AMNH; Botanical Gardens 8M, 4F AMNH; Hololo 1M AMNH; Santa Cruz 1F AMNH; Dabadie 1M, 1F AMNH; Maraval rd. 1F AMNH; No locality data 2M BMNH; 1M, 1F AME. No locality data 4M, 3F BMNH; 4M, 1F ZMHU; 1M, 1F USNM; 1M MNHN.

Theope leucanthe Bates, 1868

Figs. 66a-h; 133; 201; 257; 273.

Theope leucanthe Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 408. **TL**: Pará, E. Brazil. Syntype male and female BMNH [Examined]; Lectotype male BMNH [Designated].

Identification and Taxonomy: Average forewing length: both sexes 10.5mm.

MALE: *T. leucanthe* is geographically variable enough that it can be confused with different species in different parts of its range, but clinal intergrades exist between the extreme phenotypes, whose male genitalia do not differ, and hence no subspecies are recognised. The syntype male is actually rather abnormal and is virtually the only specimen I have seen with absolutely no blue on the DFW. Such specimens of *T. leucanthe*, from the lower Amazon, have a very similar dorsal surface to the distantly related *T. simplicia*, although the blue coloration is paler and there is a black line marking the end of each hindwing discal cell, but the ventral surface is a paler, white color and there are black spots around the distal margins of both wings that also show through onto the DHW. *T. leucanthe* is most similar to *T. amicitiae* but externally differs most notably in its slightly larger size, and by having an almost entirely blue DHW; male genitalic differences exist in the shape of the uncus, valvae and internal aedeagal structures. Specimens of *T. leucanthe* from more westerly localities, towards the base of the eastern Andes and in Panama, have increasingly more blue on the DFW and may be confused with *T. foliorum*. However, they differ by having a slightly more compact wing shape, slightly paler blue dorsal coloration that tends to form more of an apically directed triangle on the forewing than a semicircle, and a paler, whiter ventral surface that always has prominent black spots ringed by white around the distal margins of both wings. The male genitalia of *T. leucanthe* differ from those of *T. foliorum* in the shape of the uncus, the upper "arm" of the valvae and, most notably, the aedeagus, which is long, slender and tapers at the tip instead of being bulbous, a character that places the species in different subgroups; the eighth abdominal tergite of *T. leucanthe* also has no posterior projection.

FEMALE: as in the male, female *T. leucanthe* from the lower Amazon has dorsal blue restricted to the hindwing and it is distinguished from *T. simplicia* by the same characters as for the male. Specimens with some blue at the base of the DFW might be confused with *T. foliorum* but the DHW of these *T. leucanthe* females is entirely blue, the wing shape is more compact and the hindwing slightly angular and, of course, the ventral surface has prominent black spots ringed with white around the distal margins of both wings. *T. leucanthe* from the most westerly localities has a large block of blue on the DFW and thus resembles *T. hypoleuca* and *T. batesi* on the dorsal surface, but it can immediately be distinguished by the aforementioned ventral character.

Due to the uncertainty in identifying female *T. leucanthe*, with respect to the as yet unknown or at least unrecognised female of *T. amicitiae*, it seems prudent to designate the male syntype of *T. leucanthe* as a lectotype. This specimen in the BMNH bears the following labels: "leucanthe", "Theope/leucanthe./Bates./Godman-Salvin/Coll. 1914.-5.", "Para./L. Amazons./H.W. Bates", "Type, H.T.".

Biology: Nothing is known about the biology of this uncommon species.

Distribution: *T. leucanthe* is distributed widely from Panama to south and south-east Brazil, with its center of distribution being the Amazon basin. It is reported to me from Trinidad by M. Cock (pers. comm.; in the coll. of F. C. Urich) and from French Guiana by J.-Y. Gallard (pers. comm.).

Specimens Examined: 36M 12F

PANAMA: *Colón*, Portobelo 1M USNM; *Panamá*, Bayano 1F USNM; *Canal Zone*, Río Torti 1M USNM; Summit 1F AME. **VENEZUELA**: *Aragua*, Ocumare de la Costa 2M USNM; *Anzoátegui*, 10 km N.W. of Barcelona 1M, 1F USNM. **COLOMBIA**: *Valle de Cauca*, Río Tatabro 1M JS; *Meta*, Cubarral 2M JS; *Caquetá*, Montañita 1M, 1F USNM.

ECUADOR: *Napo,* km 4 Misahualli-Puerto Napo rd. (Oct) 2M RCB; Río Napo 1M BMNH; No locality data 1M, 1F BMNH. **PERU**: *Loreto*, Iquitos 2M BMNH; 3M MNHN; Pebas 1F BMNH; Caballo Cocho 1F BMNH; Río Nanay 1M MNHN; *Madre de Dios*, Parque Nacional del Manu, Pakitza 1M USNM; *Puno*, Chaquimayo 1F BMNH. **BRAZIL**: *Amazonas*, Humaitá 1M BMNH; Massauary; *Rondônia*, environs of Fazenda Rancho Grande, nr. Cacaulândia 1M NSM; *Pará*, Itaituba 1M ZMHU; Santarem 1M, 1F BMNH; Pará 1M BMNH; Igarapé-Açu 1M AMNH; Lower Amazon 1M BMNH; *Pernambuco*, São Lourenço da Mata 5M USNM; *Mato Grosso*, Cuiabá 1M BMNH; *Minas Gerais*, Barbacena 2F USNM 1M BMNH; 1M ZMHU; No locality data 1F MNHN. No locality data 1M ZMHU.

Theope amicitiae Hall, Gallard & Brévignon, 1998

Figs. 67a,b; 134; 202; 273.

Theope amicitiae Hall, Gallard & Brévignon, 1998. *Lambillionea* 98(4): 565-566, figs. 3a,b. **TL**: Galion, Roura, French Guiana. Holotype male MNHN; type illustrations [Examined].

Identification and Taxonomy: Average forewing length: male 9mm.

MALE: *T. amicitiae* most closely resembles *T. leucanthe*, especially sympatric lower Amazon specimens, because both are small and lack blue on the dorsal forewing. *T. amicitiae* differs from *T. leucanthe* by being slightly smaller, by having a more compact wing shape, blue restricted to the tornal region of the dorsal hindwing, and slightly more contrasted pale squares around the ventral submarginal black spots. On the basis of examining the male genitalia of two specimens of *T. amicitiae* and several specimens of *T. leucanthe*, from disparate geographic localities (see Appendix B), these are the consistent male genitalic differences between the two species: *T. amicitiae* has a more pronounced and rounded upper portion to the uncus, smaller falci, a small projection from the middle of the lower edge of the upper valve "arm" and, most diagnostically, numerous very small spines on the aedeagal vesica that form a broad band in the middle of the aedeagus and taper towards the tip; the vesica of *T. leucanthe* is studded with tiny sclerotised structures but lacks these larger spines.

FEMALE: unknown.

Biology: Both male types were captured in the afternoon along the forest edge near the crest of the Montagne des Chevaux (Hall, 1998a).

Distribution: *T. amicitiae* is currently only known from the two French Guianan specimens and although no others have been located in major world museum collections, it is expected to have a broader lower Amazon distribution.

Specimens Examined: 2M

FRENCH GUIANA: *Cayenne*, Galion, Roura 1M MNHN; 1M FSCA.

Theope christiani Hall & Willmott, **repl. name**

Figs. 68a,b; 135; 203; 273.

Theope brevignoni Hall & Willmott, 1996. *Trop. Lepid.* 7(1): 65-66, figs. 6a,b. **TL:** Annai, Essequibo river, Guyana. Holotype male BMNH [Examined].

Identification and Taxonomy: Forewing length: male 16mm.

The inclusion in this work of the species heretofore treated in *Parnes* in the genus *Theope* (see introductory "Taxonomy" section) brings into homonymy the name *brevignoni*, which was used for a new species of *Parnes* by Gallard (1996), and a new species of *Theope* by Hall and Willmott (1996). These two taxa were described in the same year, but since the former was described several months before the latter, I treat the former as the senior homonym. The name *christiani* Hall & Willmott is therefore provided as a replacement for the latter taxon.

MALE: *T. christiani* differs from perhaps its closest relative, *T. methemona*, by having a more pointed hindwing shape, grainy gray-blue dorsal coloration that extends to the costal margin on the hindwing (where it becomes paler), by lacking the variably sized postdiscal area of pale brown scaling on the DFW and, of course, by having a completely different ventral pattern that consists of shades of brown with two semicircular white markings around each discal cell end and one white spot above each. The male genitalia of the two species differ only minorly in the shape of the upper valve "arm" and the pattern of tiny sclerotised structures on the aedeagal vesica.

FEMALE: unknown.

Biology: Nothing is known about the biology of this very rare species.

Distribution: *T. christiani* is only known from the unique holotype from Guyana, and C. Brévignon and J.-Y. Gallard (pers. comm.) do not report finding it in French Guiana, despite many years of intensive riodinid collecting there. However, its true range surely includes at least the remaining Guianan countries and north-east Brazil.

Specimens Examined: 1M

GUYANA: *Upper Takutu/Upper Essequibo*, Annai, Essequibo river 1M BMNH.

Theope methemona Bates, 1868

Figs. 69a-f; 136; 204; 273.

Theope methemona Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 408. **TL**: Santarem, E. Brazil. Syntype male BMNH [Examined].

Identification and Taxonomy: Average forewing length: male 15mm.

MALE: *T. methemona* superficially most closely resembles *T. wallacei*, with which it shares an almost identical wing shape and ventral pattern. It differs by having a slightly paler dorsal ground color, a variably sized area of postdiscal pale brown scaling on the DFW (not visible in the syntype), a broad dark brown distal margin to the DHW and more elongate submarginal black spots on the ventral surface that are encircled with a more prominent and elongate area of white scaling, and are present on both wings. The male genitalia of the two species are quite different, placing them in different subgroups; *T. methemona* most notably has a rounded uncus, no hump at the base of the upper "arms" of the valvae, which themselves are positioned more closely together in dorsal view, and a long aedeagus of even width that lacks internal cornuti. The last abdominal tergite also has an entire posterior edge, without a small, rounded projection from the lower posterior corner.

T. methemona appears to be most closely related to *T. sticheli* and *T. christiani*, on the basis of their male genitalia being almost inseparable. *T. christiani* has a quite different ventral pattern, blue-gray dorsal coloration that extends to the costal margin of the hindwing and no pale brown postdiscal scaling on the DFW, but *T. sticheli* is more similar; it is a smaller species with a more compact wing shape, blue dorsal coloration that extends to the distal margin in the tornal region of the hindwing and forms a more even semicircle on the forewing, where there is a sickle-shaped black mark at the discal cell end.

FEMALE: unknown.

Biology: Nothing is known about the biology of this very rare species.

Distribution: *T. methemona* is only known from two nearby localities on the lower Amazon.

Specimens Examined: 3M

BRAZIL: *Pará*, Obidos 1M MNHN; Santarem 2M BMNH.

Theope sticheli Hall, 1998

Figs. 70a-d; 137; 205; 258; 273.

Theope sticheli Hall, 1998. *Lambillionea* 98(4): 566-567, figs. 4a,b. **TL**: Itaituba, Rio Tapajós, E. Brazil. Holotype male ZMHU and allotype female UFP [Examined].

Identification and Taxonomy: Average forewing length: male 13.5mm, female 13mm.

MALE: although *T. sticheli* superficially closely resembles *T. wallacei*, the male genitalia of the latter, as described in the account of that species, place it in a different subgroup. Based on wing pattern and male genitalia, *T. sticheli* can be placed closest to *T. methemona*. It differs from that species by its smaller size, compact wing shape, which has a less pointed forewing and a slightly more angular hindwing, and on the ventral surface by having slightly more rounded submarginal black spots. On the dorsal surface, it differs by having blue colouration that always extends to the distal margin on the hindwing, leaving a conspicuous triangular black area in cells M2 and M1, and a laterally constricted semicircle of blue on the forewing that has no pale brown postdiscal scaling (this is not discernible on the syntype of *T. methemona*) and a sickle-shaped black marking at the discal cell end. A similar mark is variably prominent in the upper half of the discal cell on the DHW. The male genitalia of the two species differ only minorly in the size and extent of the tiny sclerotised structures of the aedeagal vesica; those in *T. sticheli* appear to be smaller, but because the anterior section of the aedeagus is so contorted in both species, their vesicas could not be everted to make a more detailed comparison.

FEMALE: the female of *T. sticheli* was recently illustrated as a putative female of another Brazilian species, *T. turneri*, in Hall and Austin (1997), but the subsequent discovery of male specimens that essentially exactly match that female show the association to be incorrect. *T. sticheli* is distinguished from similar species, such as *T. lycaenina* and *T. wallacei*, by the same wing pattern characters as for the male and, in the genitalia, by having signae that are not serrate along their internal edge and are shorter at their opening to the corpus wall, and by not having a sclerotised or coiled posterior portion to the ductus bursae.

Biology: Nothing is known about the biology of this very rare species.

Distribution: *T. sticheli* has a broad Amazonian distribution that is currently known to encompass the area from near the base of the eastern Andes in Ecuador to south-west and east Brazil, implying its certain occurrence in Peru, and probably also Colombia and Bolivia.

Specimens Examined: 2M 1F

ECUADOR: *Sucumbíos,* Garzacocha, La Selva (Nov) 1M PJD. **BRAZIL**: *Rondônia*, environs of Fazenda Rancho Grande, nr. Cacaulândia, Rio Pardo (Aug) 1F UFP; *Pará*, Rio Tapajós, Itaituba 1M ZMHU.

Theope busbyi Hall, 1998

Figs. 71a,b; 138; 206; 273.

Theope busbyi Hall, 1998. **TL**: km 4 Misahualli-Puerto Napo rd., E. Ecuador. *Lambillionea* 98(4): 567-568, figs. 5a,b. Holotype male USNM [Examined].

Identification and Taxonomy: Forewing length: male 11mm.

MALE: the male genitalia of *T. busbyi* are very similar to and thus place the species closest to *T. christiani*, *T. methemona* and *T. sticheli*. The presence of two distinct types of sclerotised structures towards the tip of the everted aedeagal vesica is a noteworthy genitalic character, but since the vesicas of the other species could not be everted, due to the sigmoidal shape of the aedeagus, comparisons are difficult to make. The wing pattern of *T. busbyi*, which has blue extending to the very costal margin of the DHW and a broad, even dark brown outer margin to that wing, a sickle-shaped discal cell end marking only on the DFW, and a unique ventral surface for the genus that contains a scattering of two distinct scale colors, pale brown over predominantly dark brown, is utterly distinct.

FEMALE: unknown.

Biology: The holotype male was collected on a flowering bush at the forest edge (R. Busby, pers. comm.).

Distribution: This species is currently only known from the base of the eastern Andes in Ecuador, but it undoubtedly has a wider west Amazonian distribution.

Specimens Examined: 1M

ECUADOR: *Napo,* km 4 Misahualli-Puerto Napo rd. (Oct) 1M USNM.

Theope turneri Hall & Austin, 1997

Figs. 72a,b; 139; 207; 273.

Theope turneri Hall & Austin, 1997. *Trop. Lepid.* 8(2): 101-102, figs. 1a-d. **TL**: Linha C-25, off B-65, 12.5 km S. of Cacaulândia, S.W. Brazil. Holotype male UFP [Examined].

Identification and Taxonomy: Forewing length: male 13.5mm.

MALE: *T. turneri* is most similar to *T. methemona* and *T. sticheli*, but differs from both externally by having a wing shape that is more compact than *T. methemona* but not as compact as *T. sticheli*, dorsal blue coloration that is reduced to the very base of both wings and a darker ventral surface that has less prominent submarginal black spots (their presence or absence on the VFW can not be ascertained from the damaged holotype). The male genitalia of *T. turneri* differ most notably by having reduced sclerotised structures on the aedeagal vesica and a downwardly pointed instead of rounded posterior edge to the uncus which appears to be intermediate to that of *T. foliorum* and relatives, although the lower posterior corner is not heavily sclerotised as it is in those species.

FEMALE: although a putative female was illustrated for *T. turneri* in Hall and Austin (1997), it is clear now that this specimen is conspecific with the subsequently described species *T. sticheli*. The female of *T. turneri* remains unknown.

Biology: Nothing is known about the biology of this very rare species.

Distribution: *T. turneri* is currently known only from Rondônia state in the south-western Brazilian Amazon and, like *T. pakitza* and, for example, *Sarota harveyi* (see Hall, 1998b), it may have a range that is restricted to south Peru, Bolivia and south-west Brazil.

Specimens Examined: 1M

BRAZIL: *Rondônia*, environs of Fazenda Rancho Grande, 12.5 km S. of Cacaulândia 1M UFP.

Theope batesi Hall, 1998

Figs. 73a-d; 140; 208; 274.

Theope batesi Hall, 1998. *Lambillionea* 98(4): 568-569, figs. 6a,b. **TL**: Manicoré, C. Brazil. Holotype male MNHN [Examined].

Identification and Taxonomy: Average forewing length: male 10mm.

MALE: *T. batesi* has a rather non-descript wing pattern and, by virtue of having no ventral submarginal spotting, superficially resembles certain distantly related species, such as *T. simplicia*, *T. hypoleuca* and *T. azurea*, which, by virtue of lacking an elongate upper "arm" to the valvae of the male genitalia, lie outside the "*foliorum* group". *T. batesi* differs from all three in wing pattern alone by always having a prominent very thin dark brown line at the very distal margin of both ventral wings, which are also usually a darker color, and reduced blue on the DFW, which is absent in *T. simplicia* and more extensive in the other two species. Within the "*foliorum* group", *T. batesi* is unique in always lacking ventral submarginal spotting (*T. lycaenina* rarely also lacks them), and its male genitalia exhibit two autapomorphies that are unique within the genus, the tribe Nymphidiini and almost certainly the whole family Riodinidae, namely the presence of two lateral flanges either side of the tip of the aedeagus, one containing erectile androconial hairs. Other male genitalic characters that separate it from species of the main "*foliorum* group", include the presence of aedeagal cornuti, a markedly bifurcate uncus, and a considerably broader vestigial last sternite segment.

The specimen (Fig. 73a,b) of *T. batesi* from near Belém (Pará) in the eastern Amazon has a wing pattern exactly the same as the central Amazonian holotype, but the Ecuadorian specimen (Fig. 73c,d) has an entirely blue DHW except for the apex, increased blue on the DFW that nearly reaches the tornus, and a darker ventral ground color. A similar phenomenon of increased dorsal blue in west Amazonian specimens can be seen in *T.*

leucanthe. Conversely, in the male genitalia, the Ecuadorian specimen (Fig. 149 - lower right) differs relatively little from the holotype, by having three aedeagal cornuti instead of five, but the Belém specimen (Fig. 149 - lower left) has eleven aedeagal cornuti, four of which form a continuous span at the mouth of the aedeagus. Such drastic geographic variation in male genitalia is certainly highly atypical in *Theope*, but the number of aedeagal cornuti does also vary geographically in *T. wallacei*. As the two aforementioned specimens do not differ in any other significant regard from the holotype, and in the absence of any comparative ecological information, particularly life history information, I prefer for the moment to conservatively regard them as belonging to *T. batesi*.

FEMALE: unknown.

Biology: Essentially nothing is known about the biology of this species, but the Ecuadorian specimen of *T. batesi* was captured from a flowering bush at the forest edge (G. Busby, pers. comm.).

Distribution: *T. batesi* is known from disparate localities that encompass the entire length of the Amazon basin.

Specimens Examined: 3M

ECUADOR: *Napo,* km 4 Misahualli-Puerto Napo rd. (Oct) 1M GWB. **BRAZIL**: *Amazonas*, Manicoré 1M MNHN; *Pará*, Belém-Camiranga rd., Igarapé-Açu 1M AMNH.

Theope atima Bates, 1868

Figs. 74a,b; 141; 209; 274.

Theope atima Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 407. **TL**: Ega, W. Brazil. Syntype male BMNH [Examined].

Identification and Taxonomy: Average forewing length: male 12mm.

MALE: *T. atima* is most similar to *T. foliorum*; when comparing perfect specimens of each species, their wing pattern differences are quite apparent, but even faintly worn specimens of *T. atima* can be very difficult to distinguish from *T. foliorum*. The distal blue rays on the DFW of *T. atima* are rarely so clear as they are in the figured syntype specimen, but the species can still be identified by the horizontal "V"-shaped section of blue on the DFW that extends from the wing base to the end of the discal cell and along the anal margin to the tornus, and by the slightly darker ventral surface which has more prominent spots in the tornus of the VHW and consequently on the DHW. The downwardly pointed, heavily sclerotised lower posterior corner of the uncus and presence of a hump at the base of the upper valve "arms" in the male genitalia of *T. atima* place the species closest to *T. foliorum*, *T. wallacei* and *T. pakitza*. It is readily distinguished from them all by having a sharply tapered tip to the aedeagus, which opens to the left and contains several small triangular cornuti; the last abdominal tergite of *T. atima* is also unique in the "*foliorum* group" in possessing a small posteriorly projecting spike from the lower posterior corner.

FEMALE: the female of *T. atima* is currently unknown, but will undoubtedly be very difficult to separate from female *T. foliorum*.

Biology: Nothing is known about the biology of this rare species.

Distribution: *T. atima* is only known from a handful of localities on the middle and lower Amazon.

Specimens Examined: 8M

BRAZIL: *Amazonas*, Tefé 1M BMNH; Ipiranga 1M MNHN; *Pará*, Juruti 1M ZMHU; 1M MNHN; Santarem 1M ZMHU; 1M MNHN; Rio Tapajós 2M BMNH.

Theope foliorum Bates, 1868

Figs. 9; 75a-h; 142; 210; 259; 274.

Theope foliorum Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 407. **TL**: Santarem, E. Brazil. Syntype male and female BMNH [Examined]; Lectotype male BMNH [Designated].

= ***Theope punctipennis*** Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 407. **TL**: Ega, W. Brazil. Syntype female BMNH [Examined]; Lectotype female BMNH [Designated].

= ***Theope herta*** Godman & Salvin, 1886. *Biol. centr.-amer., Lep. Rhop.* 1: 483; 3: pl. 47, figs. 25, 26. **TL**: Bugaba (800-1500ft), Panama. Holotype female BMNH [Examined]. **[n. syn.]**

Identification and Taxonomy: Average forewing length: male 13mm, female 12mm.

MALE: *T. foliorum* is probably externally most similar to *T. atima*. The two species have the same wing shape, but *T. foliorum* typically has a paler ventral surface, less prominent spots in the tornus of both hindwing surfaces, and a simple semicircle of blue on the DFW without any distal blue rays. *T. foliorum* also somewhat resembles specimens of *T. leucanthe* from Panama and the western Amazon region, but it is typically larger, has a more pointed wing shape, a more semicircular blue patch on the DFW, less prominent discal cell end markings on the DHW, and, most notably, a darker dirty cream colored ventral surface that lacks black spots around the entire distal margins of both wings. The faint spots in the tornus of the VHW in *T. foliorum* separate it from *T. batesi* and the distantly related *T. hypoleuca* and *T. azurea*, which additionally differ in their dorsal surface patterns and ventral ground colors. The male genitalia of *T. foliorum* differs from those of all the above species by having a longer and more densely setose upper "arm" to the valvae, with a larger semicircular hump at its base, and a torsional, bulbous posterior end to the aedeagus. A consilience of genitalic characters places *T. foliorum* closest to *T. wallacei* and *T. pakitza*, from which it is distinguished in those species accounts.

FEMALE: females of *T. foliorum* typically have less dorsal blue, especially on the forewing, than those of similar species, such as *T. lycaenina*, *T. wallacei* and *T. leucanthe*, but some *T. foliorum* specimens may closely resemble those of *T. leucanthe* from westerly localities; they differ by having a slightly broader wing shape, a semicircle of blue at the base of the DFW instead of an apically directed triangle, less prominent black spots around the distal margin of the VFW, and no paler white circles around any ventral submarginal spots.

T. foliorum is a geographically rather variable species. Both sexes vary in size, the shade of the dorsal ground color (pale brown to black) and the ventral ground color (white to dirty cream), the number and prominence of ventral submarginal spots, and the amount of dorsal blue coloration; the upper "arm" of the valvae in the male genitalia is also slightly variable in width and shape, and the last abdominal tergite has variably prominent projections from the lower posterior corner. Specimens from Panama and northern Venezuela have blue reduced to the very base of both dorsal wing surfaces. This phenotype was described from a single female specimen as *herta* by Godman and Salvin (1886), and treated as a full species by all subsequent authors. I considered retaining *herta* as a subspecies of *T. foliorum*, but in view of the great variation exhibited by this species, even within local populations, and the fact that clinal intergrades exist throughout a wide area of north-eastern South America, especially in Venezuela, and the entire range of phenotypes exists on Trinidad, I synonymise it with *T. foliorum*. The taxon *punctipennis* was also described as a full species from both sexes, on the same page of the same work as *T. foliorum*, by Bates (1868), but the single labelled syntype, a female, differs from that of *T. foliorum* only by having a darker ventral surface and more prominent submarginal spots on the VFW. Stichel (1930) recognised that these differences were within the normal range of variation for *T. foliorum* and, as far as can be told (see below), correctly treated *punctipennis* as an infrasubspecific form of it.

Due to the uncertainty in identifying female *T. foliorum*, with respect to the as yet unknown or at least unrecognised female of *T. atima*, I designate the male syntype of *T. foliorum* as a lectotype. It bears the following labels: "foliorum", "Theope/foliorum,/Bates./ Godman-Salvin/Coll. 1914.-5.", "Santarem,/Amazons./H.W. Bates", "Type, H.T.". Although *punctipennis* was described from both sexes and two localities (Ega and Tapajós), only a single female syntype is labelled in the BMNH from Ega. To avoid confusion over the identity of this taxon, I designate this female syntype as a lectotype. It bears the following labels: "puntipennis", "Theope/puntipennis,/Bates./Godman-Salvin/Coll. 1914.-5.", "Ega,/U. Amazons./H.W. Bates", "Type, H.T.".

Biology: *T. foliorum* is widespread in a variety of forest habitats up to 1000m. It is one of very few "*foliorum* group" species to be relatively commonly represented in collections and yet essentially nothing is known of its biology. In Ecuador, a female was encountered flying low to the ground in the understory of a large forested hilltop at 1600h.

The only known life history details of *T. foliorum* were reported by Guppy (1904), who found larvae on *Theobroma cacao* (Sterculiaceae) in Trinidad. His illustration of a mature larva is reproduced here (see Fig. 9).

Distribution: *T. foliorum* occurs from Panama to the Guianas and Amazon basin, and thence as far south as south-east Brazil and Paraguay. Very few specimens in collections originate from the western Amazon and none have yet been collected in the Chocó region of west Colombia and Ecuador, where it should occur. The following additional locality is listed by Lamas *et al.* (1991) for PERU: *Loreto*, Castaña.

Specimens Examined: 84M 110F

PANAMA: *Chiriquí*, Bugaba 1F BMNH; No specific locality 2F ZMHU; *Panamá*, Cañita 1F USNM; *Canal Zone*, Summit 1F USNM; Madden 2M USNM; Gamboa 4M, 3F AME; Ft. Clayton 2M USNM; Cocoli 1M, 1F USNM; Piña 2M USNM; 3F AME; Paraiso 1F AME; Río Torti 1F USNM; Barro Colorado Is. 1F AMNH; Gatun 1F AMNH. **VENEZUELA**: *Distrito Federal*, Río Camuri 1M, 2F AME; *Aragua*, El Limón 1M AME; Cata Cuyagua 1M AME; *Carabobo*, San Esteban Valley 6M, 11F BMNH; Puerto Cabello 1F BMNH; 3M, 2F ZMHU; Valencia 1M BMNH; *Sucre*, Carúpano 1M BMNH; Campo Claro 1M, 1F AMNH; *Monagas*, Caicara 2M, 4F BMNH; *Bolívar*, Ciudad Bolívar 3M, 3F BMNH; 1F AMNH; No locality data 1F BMNH; 1F ZMHU. **COLOMBIA**: *Caldas*, Victoria 1F USNM; ? Caucathal 1M MNHN; No locality data 1M BMNH. **ECUADOR**: *Pastaza,* 14 km S. of Shell (Oct) 1M GWB; *Napo,* km 4 Misahualli-Puerto Napo rd. (Oct) 1M, 1F RCB; Apuya (Sept) 1F JHKW. **PERU**: *Ucayali*, Pucallpa 3M, 1F AME; *Madre de Dios*, nr. Puerto Maldonado 7M, 11F USNM. **BRAZIL**: *Amazonas*, Tabatinga 1F ZMHU; Tefé 1F BMNH; Manicoré 1F ZMHU; *Rondônia*, environs of Fazenda Rancho Grande, nr. Cacaulândia 1M NSM; *Pará*, Obidos 1F ZMHU; Santarem 4M, 2F BMNH; Juruti 1M ZMHU; Pará 2M BMNH; 1M ZMHU; Igarapé-Açu 1M, 3F AMNH; 1M AME; Amazons 1M ZMHU; *Mato Grosso*, Chapada 1F BMNH; 1M MCZ; Cuiabá 1F BMNH; Diamantino 1F BMNH; 1M, 3F USNM; Corumbá 1F BMNH; *Paraíba*, João Pessoa 1F USNM; *Espiríto Santo*, Linhares 1M AME; Conceiçao da Barra 1F USNM; *São Paulo*, Campo Alegre, Itirapina 1F USNM; No locality data 2F ZMHU. **PARAGUAY**: *Caaguazu*, San José 1F BMNH; No locality data 1F USNM. **GUYANA**: *Upper Demerara/Berbice*, Wismar 1F AMNH. **SURINAM**: *Para*, Afobaka 1F USNM. **FRENCH GUIANA**: *Cayenne*, Cayenne 1M, 2F BMNH; 2M USNM; Route de L'est 1M, 1F USNM; *Saint Laurent du Maroni*, Saint

Laurent du Maroni 1M, 1F BMNH; 1M MNHN; 2F USNM; No locality data 2M, 1F BMNH. **TRINIDAD**: Port of Spain 1F MNHN; 1F AME; 1F MCZ; St. Annes 1F MNHN; Tunapuna 1M AME; 6 mi. N.W. of Arima 1F AME; Trois 1M, 1F AME; Hololo 2F AMNH; Botanical Gardens 1F AMNH; Santa Cruz 1F AMNH; Piaris 1F MCZ; No locality data 2M BMNH; 1F AME; 1F AMNH. No locality data 4M, 3F BMNH; 2F ZMHU; 1M AME; 1M, 1F MNHN; 1M, 1F USNM; 5M AMNH.

Theope wallacei Hall, 1998

Figs. 4; 76a-f; 143; 211; 260; 274.

Theope wallacei Hall, 1998. *Lambillionea* 98: 562-564, figs. 1a-d. **TL**: Piña, Canal Zone, Panama. Holotype male and allotype female FSCA [Examined].

Identification and Taxonomy: Average forewing length: both sexes 14.5mm.

MALE: *T. wallacei* superficially most closely resembles *T. methemona*, with which it shares a very similar wing shape and wing pattern. *T. wallacei* differs on the dorsal surface by never having pale brown postdiscal scaling on the forewing (this is not discernible on the syntype of *T. methemona*) and by having more extensive blue coloration on both wings but with none in cell Sc+R1 of the hindwing; on the ventral surface, the black submarginal spots are round instead of elongate, larger on the hindwing, and only have paler encircling coloration on those Amazonian specimens with darker ventral ground colors. Other superficially similar species include *T. lycaenina* and *T. sticheli*, but the wing shape of both is more rounded, the pattern of dorsal blue is different, as is the prominence and extent of the ventral submarginal spotting.

In fact, the male genitalia of *T. wallacei* are so distinct from those of any of the aforementioned taxa as to place the species in a separate subgroup. Instead of having a long, evenly narrow aedeagus, *T. wallacei* has an aedeagus with a large, semi-sclerotised, sculptured "basket"-shaped posterior portion and peg-like internal cornuti, and a hump at the base of the upper valve "arm"; *T. foliorum* and *T. pakitza* are the only other species to share both these characters. *T. wallacei* differs from *T. pakitza* by lacking white rays on the DHW, by having black costal, and typically distal, margins and a blue instead of white anal margin on the DHW, a larger semicircle of blue on the DFW, typically a slightly darker ventral ground color (this is much darker in sympatric Amazonian specimens), prominent black submarginal spots on both ventral wing surfaces, and at least three internal aedeagal cornuti in the male genitalia instead of one. *T. foliorum* is typically a smaller species, with paler dorsal blue coloration that is much reduced on the forewing and less prominent ventral submarginal black spots that are largely restricted to the hindwing; the male genitalia of *T. foliorum* differ most noticeably by having a much longer, heavily setose upper "arm" to the valvae, with a very large basal hump, a dorso-ventrally elongate basal portion to the valvae, and a more internally torsional posterior portion to the aedeagus, which has a narrower semi-sclerotised portion, typically with two small spines towards the tip.

Specimens of *T. wallacei* from French Guiana exhibit the same wing pattern as those nominotypical specimens from Panama, but the aedeagus of the male genitalia of the one dissected male contains eight internal cornuti instead of the three to five found in two dissected Panamanian specimens. Specimens from the west Amazon have a darker gray ventral ground color and thus paler coloration is apparent encircling the submarginal black spots, which are barely discernible on the forewing. Both of the Peruvian males are also considerably smaller than average; they both have five internal aedeagal cornuti.

FEMALE: of the known "*foliorum* group" females, *T. wallacei* is probably most similar to *T. lycaenina* and *T. sticheli*, but *T. wallacei* is slightly larger, has a more pointed wing shape much like that of the male, blue on the DFW that is intermediate in extent between that of *T. lycaenina* and *T. sticheli*, slightly more extensive blue on the DHW, especially in the apical region, and typically more prominent and contrasted black spots on the VHW. There are also genitalic differences in the shape of the ostium bursae, posterior portion of the ductus bursae and the signae.

Biology: Essentially nothing is known about the biology of this species, but a female was found in Ecuador feeding on low weedy flowers at the edge of secondary forest at 1500h.

Distribution: *T. wallacei* has a broad range that extends from Panama to the Guianas and thence to the base of the Andes in Ecuador and Peru, although no specimens are currently known from the Brazilian Amazon. The vast majority of known specimens originate from Panama.

Specimens Examined: 14M 24F

PANAMA: *Canal Zone*, Piña 3M, 10F AME; 2M, 5F FSCA; 3M, 1F USNM; Gamboa 1F FSCA; Gatun 2M, 3F USNM; Paraiso 1F USNM. **COLOMBIA**: *Antioquia*, Apartadó 1F ESM. **ECUADOR**: *Morona-Santiago,* San José de Morona (Sept) 1F JHKW. **PERU**: *Madre de Dios*, Parque Nacional del Manu, Pakitza 2M USNM. **FRENCH GUIANA**: *Cayenne*, Cayenne 1F BMNH; 1M USNM; No locality data 1M BMNH.

Theope pakitza Hall & Harvey, 1998

Figs. 77a,b; 144; 212; 274.

Theope pakitza Hall & Harvey, 1998. *Lambillionea* 98: 564-565. **TL**: Parque Nacional del Manu, Pakitza, 12°07'S 70°58'W, Peru. Holotype male to be deposited in the MUSM [Examined].

Identification and Taxonomy: Forewing length: male 15mm.

MALE: the presence of a large, semi-sclerotised, sculptured "basket"-shaped posterior portion to the aedeagus of the male genitalia places *T. pakitza* in a subgroup of the "*foliorum* group" that includes *T. wallacei* and *T. foliorum*. The latter has a more compact and pointed wing shape, a darker ventral ground color, prominent black submarginal spots on both hindwing surfaces and grayish blue dorsal coloration that is not as extensive in the costal area of the hindwing or the discal area of the forewing. Based on male genitalia and wing pattern, *T. pakitza* appears to be most closely related to *T. wallacei* from which it is separated in the account of that species.

FEMALE: unknown.

Biology: Nothing is known about the biology of this very rare species which, despite intensive collecting at the type locality (Lamas *et al.*, 1991; Robbins *et al.*, 1996), is still only known from the unique holotype. At the type locality, it occurs sympatrically with its two closest relatives, *T. wallacei* and *T. foliorum*.

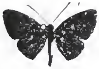
Distribution: *T. pakitza* is thus far only known from south-east Peru, but it should be looked for throughout the south-western Amazon.

Specimens Examined: 1M

PERU: *Madre de Dios*, Parque Nacional del Manu, Pakitza (Sept) 1M MUSM.

Figs. 8-9. **8**. Habitats of *Theope*. Background: tropical wet lowland forest (400m), Río Misahualli, Napo Province, east Ecuador. Inset bottom left: premontane wet forest (1600m), Río Abanico, Morona-Santiago Province, east Ecuador. Inset bottom right: tropical dry forest (800m), nr. Mácara, Loja Province, south-west Ecuador. **9**. *Theope* larval morphology adapted from Guppy (1904) (inset middle right - note constituent parts are not to scale). Bottom left: fifth instar larva of *Theope foliorum*. Upper left and middle: fifth instar larva of *Theope eudocia*; right: detail of prothoracic balloon-setae of *Theope eudocia*.

Figs. 10-17. **Group I. 10**. *T. nycteis*, male, Ega, Brazil [BMNH]: a) DS; b) VS. Male, Paneiras, Brazil [BMNH]: c) DS; d) VS. Female, Santarem, Brazil [BMNH]: e) DS; f) VS. **11**. *T. brevignoni*, male, Finca San Carlo, Ecuador [JHKW]: a) DS; b) VS. **12**. *T. philotes*, male, Ega, Brazil [BMNH]: a) DS; b) VS. Female, Amazon, Brazil [BMNH]: c) DS; d) VS. **Group II. 13**. *T. tetrastigma*, male, Apuya, Ecuador [JHKW]: a) DS; b) VS. Female, Finca San Carlo, Ecuador [JHKW]: c) DS; d) VS. **14**. *T. orphana*, male HT, Massauary, Brazil [ZMHU]: a) DS; b) VS. **Group III. 15**. *T. hypoleuca*, male, Apuya, Ecuador [JHKW]: a) DS; b) VS. Male ST, Santarem, Brazil [BMNH]: c) DS; d) VS. Female ST, Santarem, Brazil [BMNH]: e) DS; f) VS. **16**. *T. simplicia*, male ST, Pará, Brazil [BMNH]: a) DS; b) VS. Female ST, Pará, Brazil [BMNH]: c) DS; d) VS. **17**. *T. azurea* male, Finca San Carlo, Ecuador [JHKW]: a) DS; b) VS. Female, Pumayacu, Peru [AMNH]: c) DS; d) VS.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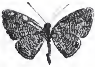
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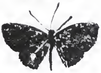
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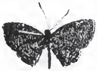
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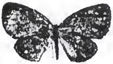
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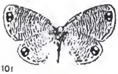
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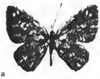
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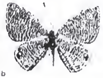
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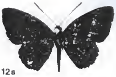
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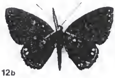
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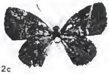
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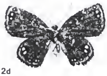
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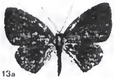
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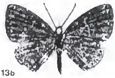
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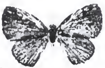
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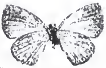
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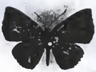
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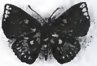
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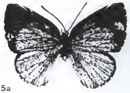
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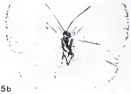
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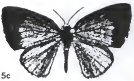
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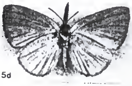
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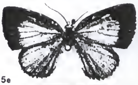
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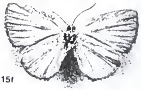
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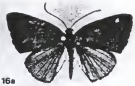
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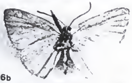
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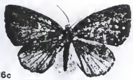
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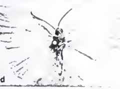
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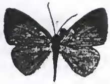
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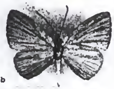
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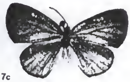
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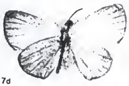
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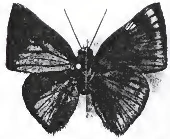
Figs. 18-22. **Group IV**. **18**. *T. a. archimedes*, male, French Guiana [USNM]: a) DS; b) VS. Female, Rio Tapajós, Brazil [BMNH]: c) DS; d) VS. *T. a. zyzyxoxyx*, HT male, Colombia [BMNH]: e) DS; f) VS. Female, Las Quiguas, Venezuela [BMNH]: g) DS; h) VS. **19**. *T. m. matuta*, male, Gatun, Panama [USNM]: a) DS; b) VS. Female HT, Santa Clara Valley, Costa Rica [BMNH]: c) DS; d) VS. *T. m. heureka* n. subsp., HT male, Bogota, Colombia [BMNH]: e) DS; f) VS. Female AT, Cananche, Colombia [BMNH]: g) DS; h) VS. **Group V**. **20**. *T. pseudopedias* n. sp., HT male, Cuyaga, Guatemala [USNM]: a) DS; b) VS. Female AT, Cuyaga, Guatemala [USNM]: c) DS; d) VS. **21**. *T. pedias*, male, Caballo Cocho, Peru [BMNH]: a) DS; b) VS. Female, nr. Cacaulândia, Brazil [NSM]: c) DS; d) VS. Female, São Paulo de Olivença, Brazil [BMNH]: e) DS; f) VS. **22**. *T. devriesi*, HT male, Guapiles, Costa Rica [BMNH]: a) DS; b) VS. Female AT, Colón, Panama [FSCA]: c) DS; d) VS.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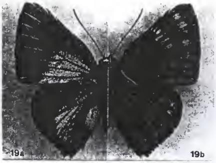
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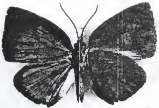
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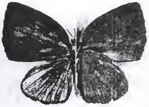
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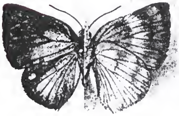
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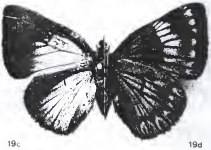
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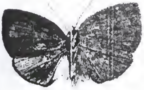
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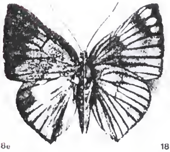
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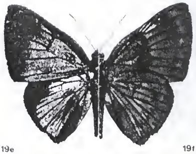
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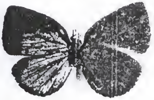
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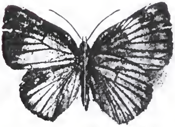
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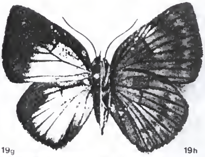
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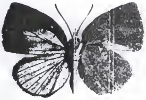
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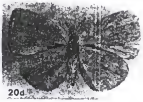
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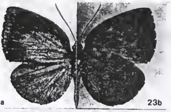
Figs. 23-29. **Group V. 23**. *T. pepo*, HT male, nr. Lita, Ecuador [JHKW]: a) DS; b) VS. Female, nr. Lita, Ecuador [JHKW]: c) DS; d) VS. **Group VI. 24**. *T. eudocia*, male, Tarapoto, Peru [BMNH]: a) DS; b) VS. Female, Santa Cruz, Brazil [BMNH]: c) DS; d) VS. **25**. *T. acosma*, male, Apuya, Ecuador [JHKW]: a) DS; b) VS. Male, Potrerillos, Panama [USNM]: c) DS; d) VS. Female, Potrerillos, Panama [USNM]: e) DS; f) VS. **Group VII. 26**. *T. excelsa*, male, Apuya, Ecuador [JHKW]: a) DS; b) VS. Female, Pará, Brazil [BMNH]: c) DS; d) VS. **27**. *T. kingi*, HT male, Gatun, Panama [USNM]: a) DS; b) VS. Female AT, Gatun, Panama [USNM]: c) DS; d) VS. **28**. *T. barea*, male, Finca San Carlo, Ecuador [JHKW]: a) DS; b) VS. Male, Gamboa, Panama [AME]: c) DS; d) VS. Female, El Llano, Panama [USNM]: e) DS; f) VS. Female, French Guiana [BMNH]: g) DS; h) VS. **29**. *T. mundula*, male, Cerro Campana, Panama [USNM]: a) DS; b) VS. Female, Cerro Campana, Panama [USNM]: c) DS; d) VS. Male, Apuya, Ecuador [JHKW]: e) DS; f) VS. Female, Finca San Carlo, Ecuador [JHKW]: g) DS; h) VS.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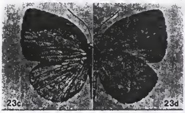
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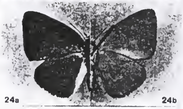
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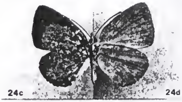
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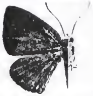
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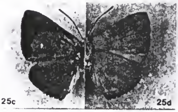
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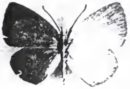
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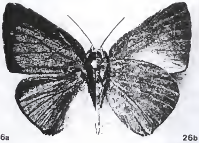
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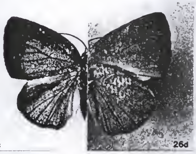
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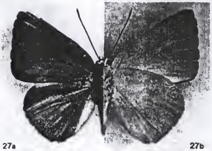
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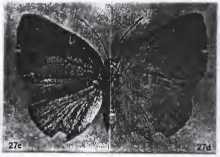
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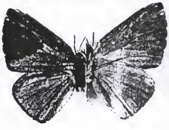
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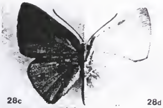
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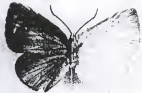
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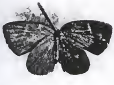
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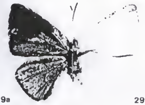
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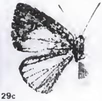
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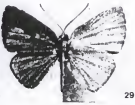
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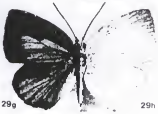
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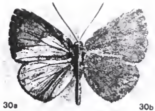
Figs. 30-38. **Group VII. 30**. *T. aureonitens*, male, Río Tiputini, Ecuador [JHKW]: a) DS; b) VS. Female, Ega, Brazil [BMNH]: c) DS; d) VS. **31**. *T. galionicus*, male, Ipiranga, Brazil [MNHN]: a) DS; b) VS. Female, French Guiana [BMNH]: c) DS; d) VS. **32**. *T. dabrerai*, male, Chichicorrumi, Ecuador [JHKW]: a) DS; b) VS. **33**. *T. sericea*, male, Amazon, Brazil [BMNH]: a) DS; b) VS. Male, Bartica, Guyana [BMNH]: c) DS; d) VS. Female, Maranhão, Brazil [BMNH]: e) DS; f) VS. **34**. *T. lampropteryx*, male, Río Tiputini, Ecuador [JHKW]: a) DS; b) VS. **Group VIII. 35**. *T. eurygonina*, male, Río San Juan, Colombia [BMNH]: a) DS; b) VS. Female, Apuya, Ecuador [JHKW]: c) DS; d) VS. **36**. *T. speciosa*, male (HT *fasciata*), No locality data [BMNH]: a) DS; b) VS. Female, km 17 San Lorenzo-Lita rd., Ecuador [JHKW]: c) DS; d) VS. **37**. *T. pieridoides*, male, La Chima, Ecuador [BMNH]: a) DS; b) VS. Female, Cuiabá, Brazil [BMNH]: c) DS; d) VS. **38**. *T. cratylus*, male, La Cambre, Honduras [BMNH]: a) DS; b) VS. Female, Chiriquí, Panama [BMNH]: c) DS; d) VS.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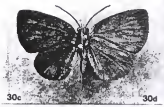
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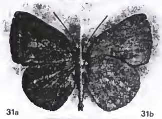
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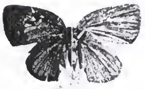
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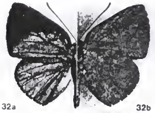
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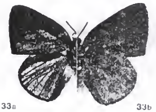
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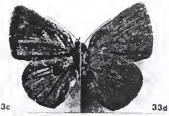
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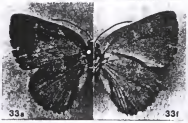
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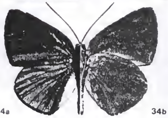
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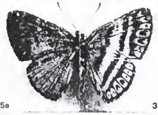
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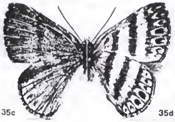
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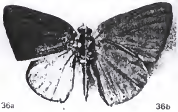
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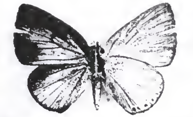
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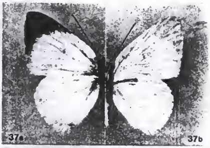
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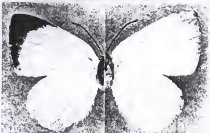
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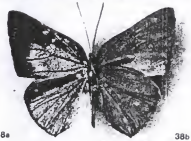
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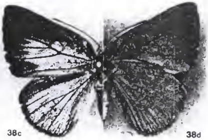
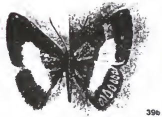

38c 38d

Figs. 39-46. **Group IX. 39**. *T. s. sisemina*, male, km 40/55 Loja-Zamora rd., Ecuador [SA]: a) DS; b) VS. Male, Baeza, Ecuador [JHKW]: c) DS; d) VS. Male, km 9 La Bonita-Rosa Florida rd., Ecuador [JHKW]: e) DS; f) VS. Female, Baeza, Ecuador [USNM]: g) DS; h) VS. *T. s. tabacona*, HT male, Río Tabaconas, Peru [BMNH]: i) DS; j) VS. **40**. *T. antanitis*, ST male, Bolivia [BMNH]: a) DS; b) VS. **Group X. 41**. *T. iani*, male, Plan Alto, Colombia [JHKW]: a) DS; b) VS. Male, La Punta, Ecuador [JHKW]: c) DS; d) VS. Female, La Punta, Ecuador [JHKW]: e) DS; f) VS. **42**. *T. villai*, female, Acahuizotla, Mexico [AME]: a) DS; b) VS. **43**. *T. virgilius*, male, Qbda. Curichanga, Ecuador [JHKW]: a) DS; b) VS. Male, Finca San Carlo, Ecuador [JHKW]: c) DS; d) VS. Female, Belize [BMNH]: e) DS; f) VS. **44**. *T. eupolis*, male, Colima, Mexico [BMNH]: a) DS; b) VS. Female, Jalapa, Mexico [BMNH]: c) DS; d) VS. **Group XI. 45**. *T. nobilis*, male, French Guiana [BMNH]: a) DS; b) VS. **46**. *T. sanjuani*, HT male, Río San Juan, Colombia [BMNH]: a) DS; b) VS.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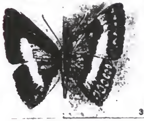
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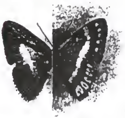
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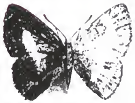
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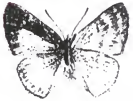
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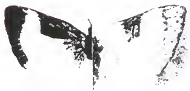
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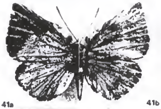
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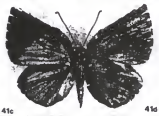
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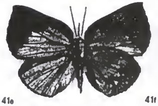
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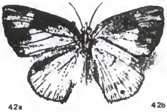
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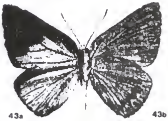
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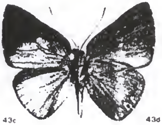
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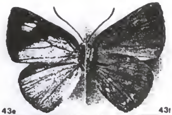
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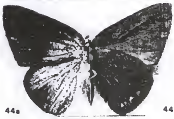
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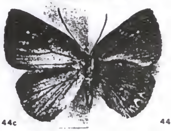
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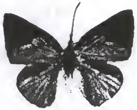
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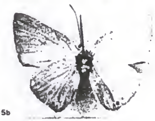
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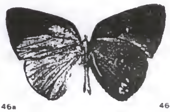
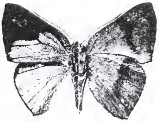

46a 46b

Figs. 47-51. **Group XI**. **47**. *T. p. publius*, male, Limón, Costa Rica [BMNH]: a) DS; b) VS. Female, Panama [BMNH]: c) DS; d) VS. *T. p. incompositus* n. subsp., HT male, nr. El Treinte, Mexico [AME]: e) DS; f) VS. Female AT, Acahuizotla, Mexico [AME]: g) DS; h) VS. Gynandromorph, Lago de Ilopango, El Salvador [AME]: i) DS. **48**. *T. syngenes*, male, French Guiana [USNM]: a) DS; b) VS. Female, French Guiana [USNM]: c) DS; d) VS. **49**. *T. terambus*, male, Rio de Janeiro, Brazil [BMNH]: a) DS; b) VS. Female, Rio de Janeiro, Brazil [BMNH]: c) DS; d) VS. **50**. *T. bacenis*, male, Guerrero, Mexico [BMNH]: a) DS; b) VS. Female (HT *mania*), San Blas, Mexico [BMNH]: c) DS; d) VS. Male, Calobre, Panama [BMNH]: e) DS; f) VS. Female, Limón, Costa Rica [BMNH]: g) DS; h) VS. **51**. *T. basilea*, male, Río San Juan, Colombia [BMNH]: a) DS; b) VS. Female ST, Río San Juan, Colombia [BMNH]: c) DS; d) VS.



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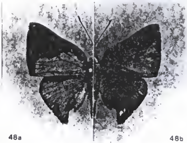

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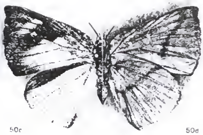

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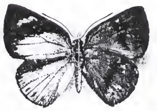

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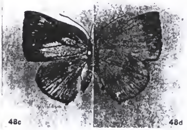

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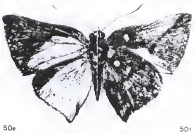

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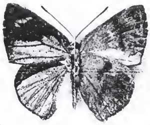

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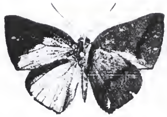

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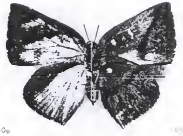

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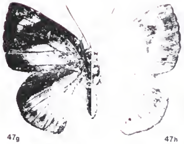
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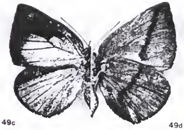
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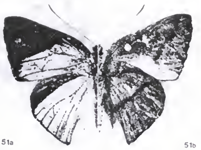
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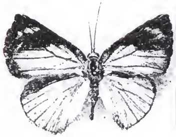
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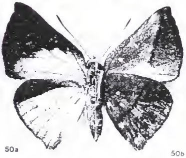
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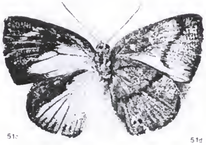
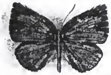

51c 51d

Figs. 52-59. **Group XII**. **52**. *T. zostera*, male, Apuya, Ecuador [JHKW]: a) DS; b) VS. Female ST, São Paulo de Olivença, Brazil [BMNH]: c) DS; d) VS. **53**. *T. nodosus* n. sp., male HT, Finca San Carlo, Ecuador [JHKW]: a) DS; b) VS. **54**. *T. sobrina*, male, Finca San Carlo, Ecuador [JHKW]: a) DS; b) VS. Female, Finca San Carlo, Ecuador [JHKW]: c) DS; d) VS. **55**. *T. comosa*, male, nr. Coca, Ecuador [JHKW]: a) DS; b) VS. Female, nr. Cacaulândia, Brazil [NSM]: c) DS; d) VS. **56**. *T. phaeo*, male, Finca San Carlo, Ecuador [JHKW]: a) DS; b) VS. Male, Río Tanti, Ecuador [JHKW]: c) DS; d) VS. Female, Río Tanti, Ecuador [JHKW]: e) DS; f) VS. **57**. *T. theritas*, male, Manicoré, Brazil [ZMHU]: a) DS; b) VS. Female, Rio Tapajós, Brazil [BMNH]: c) DS; d) VS. **58**. *T. thootes*, male, Cacaulândia, Brazil [NSM]: a) DS; b) VS. Female, Cacaulândia, Brazil [NSM]: c) DS; d) VS. **59**. *T. apheles*, male, Finca San Carlo, Ecuador [JHKW]: a) DS; b) VS. Female, Iquitos, Peru [BMNH]: c) DS; d) VS.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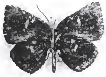
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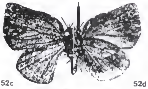
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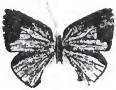
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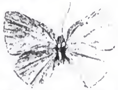
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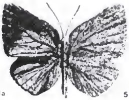
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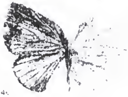
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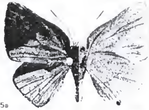
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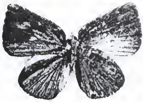
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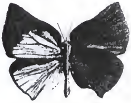
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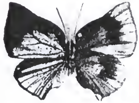
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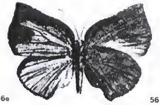
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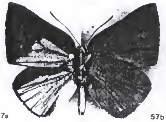
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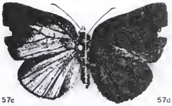
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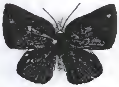
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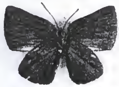
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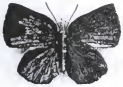
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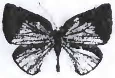
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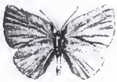
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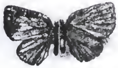
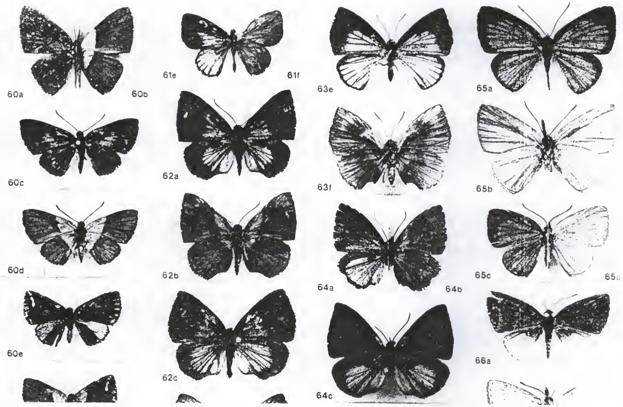

59c 59d

Figs. 60-66. **Group XIII**. **60**. *T. janus*, male, Iquitos, Peru [MNHN]: a) DS; b) VS. Male ST, Maranhão, Brazil [BMNH]: c) DS; d) VS. Female, Pará, Brazil [BMNH]: e) DS; f) VS. **61**. *T. g. guillaumei*, female, nr. Cacaulândia, Brazil [NSM]: a) DS; b) VS. *T. g. cecropia*, male, Río Blanco-Petroleo rd., Costa Rica [USNM]: c) DS; d) VS. Female HT, Finca La Selva, Costa Rica [AMNH]: e) DS; f) VS. **62**. *T. discus*, male, Pará, Brazil [BMNH]: a) DS; b) VS. Female, Iquitos, Peru [BMNH]: c) DS; d) VS. **63**. *T. thestias*, male, French Guiana [BMNH]: a) DS; b) VS. Male, Rio Grande do Sul, Brazil [BMNH]: c) DS; d) VS. Female, Iguaçu, Brazil [BMNH]: e) DS; f) VS. **64**. *T. decorata*, male, nr. Lita, Ecuador [JHKW]: a) DS; b) VS. Male, Bugaba, Panama [USNM]: c) DS; d) VS. Female, Bugaba, Panama [BMNH]: e) DS; f) VS. Female, French Guiana [BMNH]: g) DS; h) VS. **Group XIV**. **65**. *T. lycaenina*, male, Finca San Carlo, Ecuador [JHKW]: a) DS; b) VS. Female, Pará, Brazil [BMNH]: c) DS; d) VS. **66**. *T. leucanthe*, LT male, Pará, Brazil [BMNH]: a) DS; b) VS. Female, Santarem, Brazil [BMNH]: c) DS; d) VS. Male, nr. Cacaulândia, Brazil [NSM]: e) DS; f) VS. Female, Caballo Cocho, Peru [BMNH]: g) DS; h) VS.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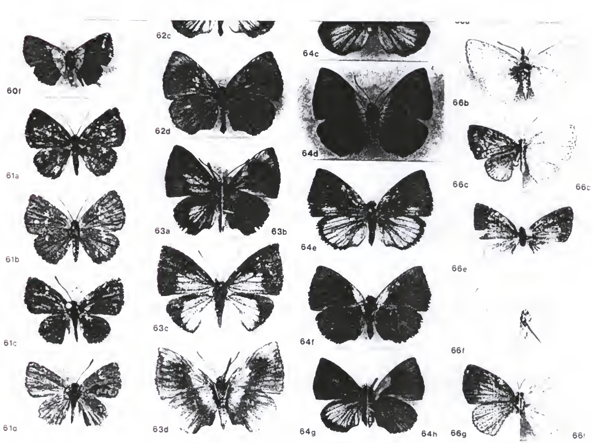
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64f
66f
61d
63d
64g
64h
66g
66f

Figs. 67-77. **Group XIV**. **67**. *T. amicitiae*, HT male, Galion, French Guiana [MNHN]: a) DS; b) VS. **68**. *T. christiani*, HT male, Annai, Guyana [BMNH]: a) DS; b) VS. **69**. *T. methemona*, ST male, Santarem, Brazil [BMNH]: a) DS; b) VS. Male, Santarem, Brazil [BMNH]: c) DS; d) VS. Male, Obidos, Brazil [MNHN]: e) DS; f) VS. **70**. *T. sticheli*, male, Garzacocha, Ecuador [PJD]: a) DS; b) VS. Female AT, nr. Cacaulândia, Brazil [UFP]: c) DS; d) VS. **71**. *T. busbyi*, HT male, km 4 Misahualli-Puerto Napo rd., Ecuador [USNM]: a) DS; b) VS. **72**. *T. turneri*, HT male, nr. Cacaulândia, Brazil [UFP]: a) DS; b) VS. **73**. *T. batesi*, male, Igarapé-Açu, Brazil [AMNH]: a) DS; b) VS. Male, km 4 Misahualli-Puerto Napo rd., Ecuador [GWB]: c) DS; d) VS. **74**. *T. atima*, ST male, Ega, Brazil [BMNH]: a) DS; b) VS. **75**. *T. foliorum*, male, San Esteban, Venezuela [BMNH]: a) DS; b) VS. Female, San Esteban, Venezuela [BMNH]: c) DS; d) VS. Male, Ciudad Bolívar, Venezuela [BMNH]: e) DS; f) VS. Female, Ciudad Bolívar, Venezuela [BMNH]: g) DS; h) VS. **76**. *T. wallacei*, male, Pakitza, Peru [USNM]: a) DS; b) VS. HT male, Piña, Panama [FSCA]: c) DS; d) VS. Female AT, Piña, Panama [FSCA]: e) DS; f) VS. **77**. *T. pakitza*, HT male, Pakitza, Peru [MUSM]: a) DS; b) VS.

67a

67b

68a

68b

70a

70b

70c

73a

73b

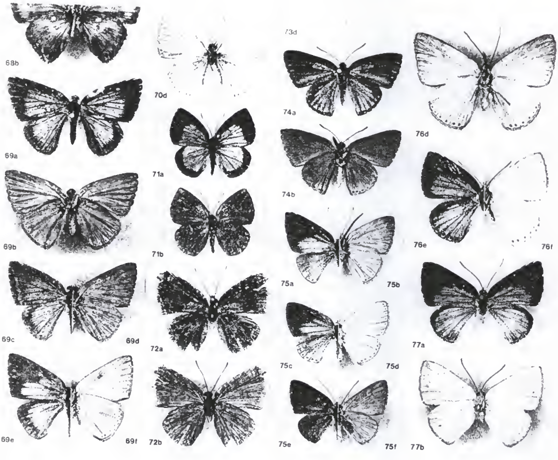
73c

73d

75g 75h

76a 76b

76c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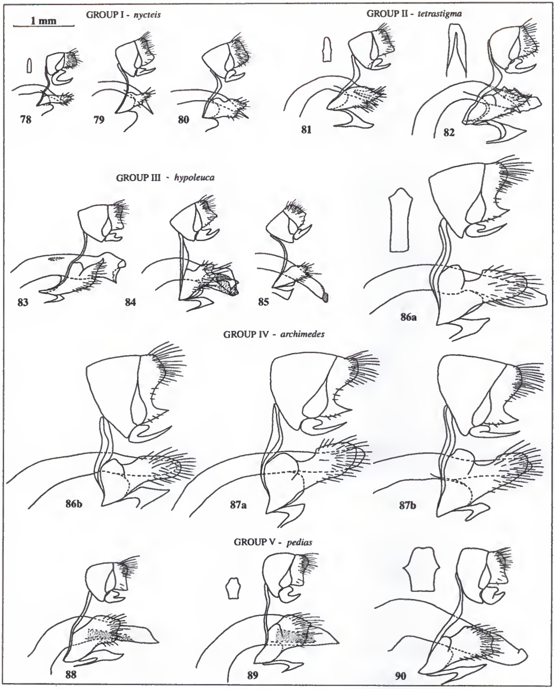
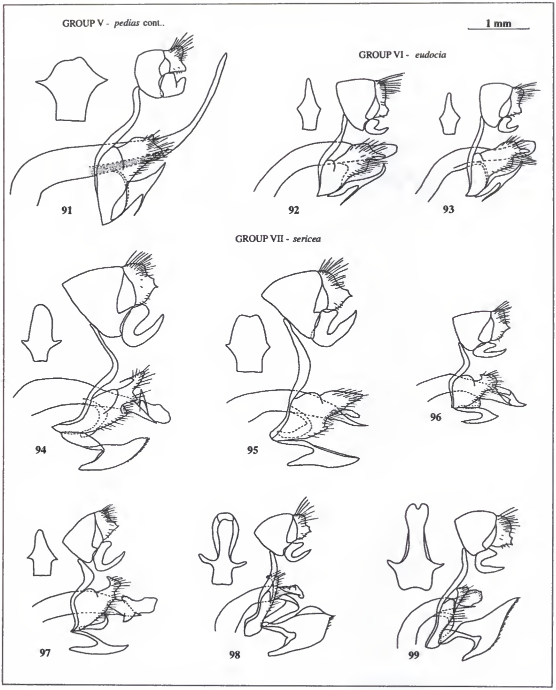
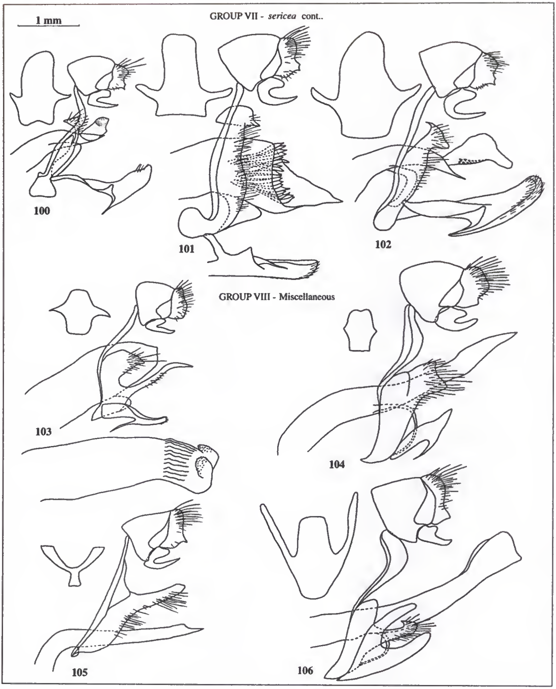


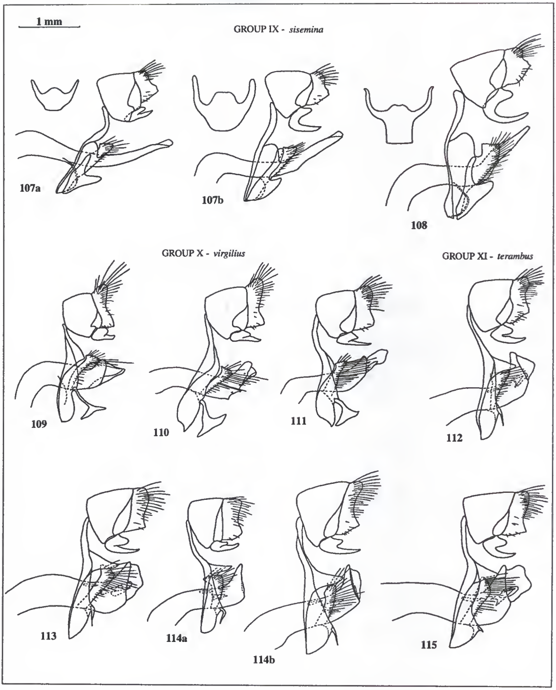
Figs. 78-90. Male genitalia in lateral view. Unless otherwise stated, accompanying structures represent the last male sternite in ventral view. See Appendix B for specimen data. **78**. *T. nycteis*. **79**. *T. brevignoni*. **80**. *T. philotes*. **81**. *T. tetrastigma*. **82**. *T. orphana*; and dorsal view of aedeagal tip (left). **83**. *T. hypoleuca*. **84**. *T. simplicia*. **85**. *T. azurea*. **86**. a) *T. a. archimedes*; b) *T. a. zyzyxoxyx*. **87**. a) *T. m. matuta*; b) *T. m. heureka* n. ssp.. **88**. *T. pseudopedias* n. sp.. **89**. *T. pedias*. **90**. *T. devriesi*.



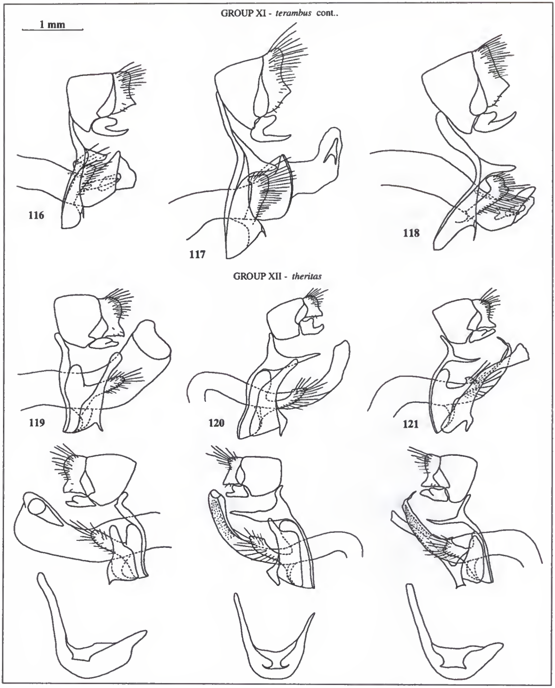
Figs. 91-99. Male genitalia in lateral view. Accompanying structures represent the last male sternite in ventral view. See Appendix B for specimen data. **91**. *T. pepo*. **92**. *T. eudocia*. **93**. *T. acosma*. **94**. *T. excelsa*. **95**. *T. kingi*. **96**. *T. barea*. **97**. *T. mundula*. **98**. *T. aureonitens*. **99**. *T. galionicus*.



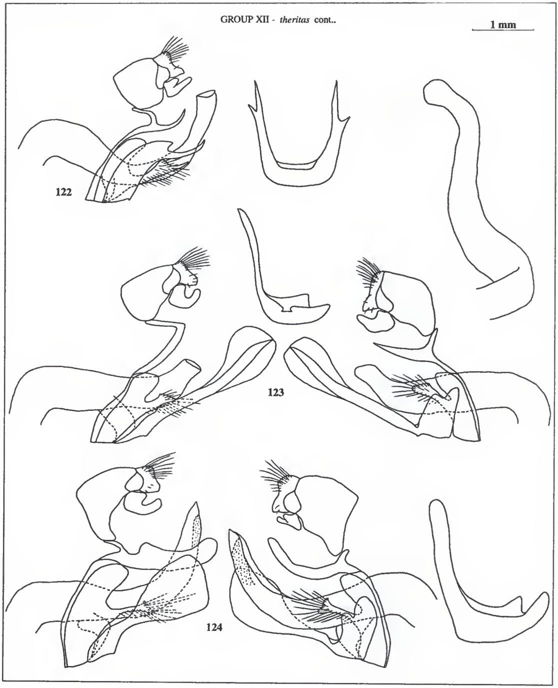
Figs. 100-106. Male genitalia in lateral view. Unless otherwise stated, accompanying structures represent the last male sternite in ventral view. See Appendix B for specimen data. **100**. *T. dabrerai*. **101**. *T. sericea*. **102**. *T. lampropteryx*. **103**. *T. eurygonina*; and aedeagus with vesica everted (below). **104**. *T. speciosa*. **105**. *T. pieridoides*. **106**. *T. cratylus*.



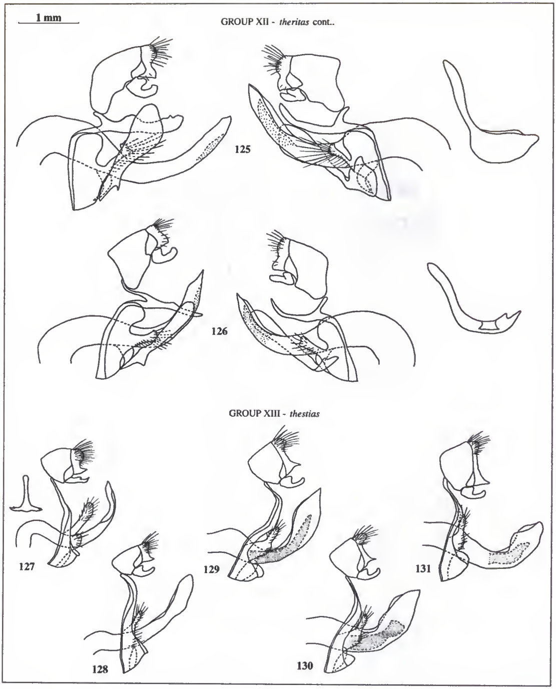
Figs. 107-115. Male genitalia in lateral view. Accompanying structures represent the last male sternite in ventral view. See Appendix B for specimen data. **107**. a) *T. s. sisemina*; b) *T. s. tabacona*. **108**. *T. antanitis*. **109**. *T. iani*. **110**. *T. virgilius*. **111**. *T. eupolis*. **112**. *T. nobilis*. **113**. *T. sanjuani*. **114**. a) *T. p. publius*; b) *T. p. incompositus* n. ssp.. **115**. *T. syngenes*.



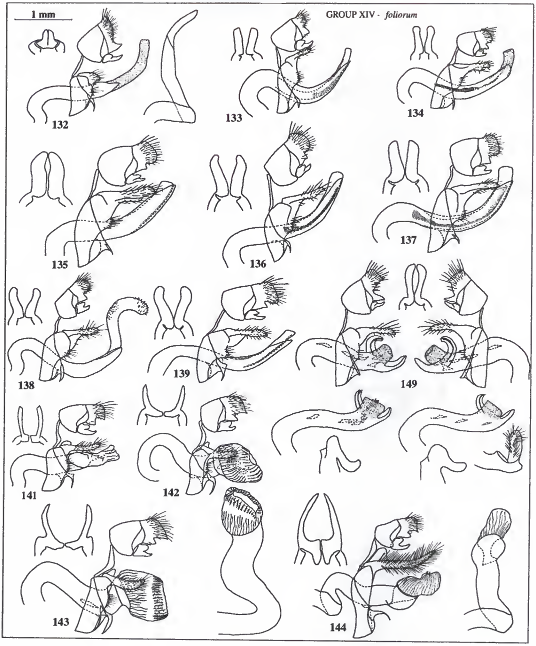
Figs. 116-121. Male genitalia in lateral view (both left and right lateral views for figs. 119-121). Accompanying structures represent the last male sternite in ventral view. See Appendix B for specimen data. **116**. *T. terambus*. **117**. *T. bacenis*. **118**. *T. basilea*. **119**. *T. zostera*. **120**. *T. nodosus* n. sp.. **121**. *T. comosa*.



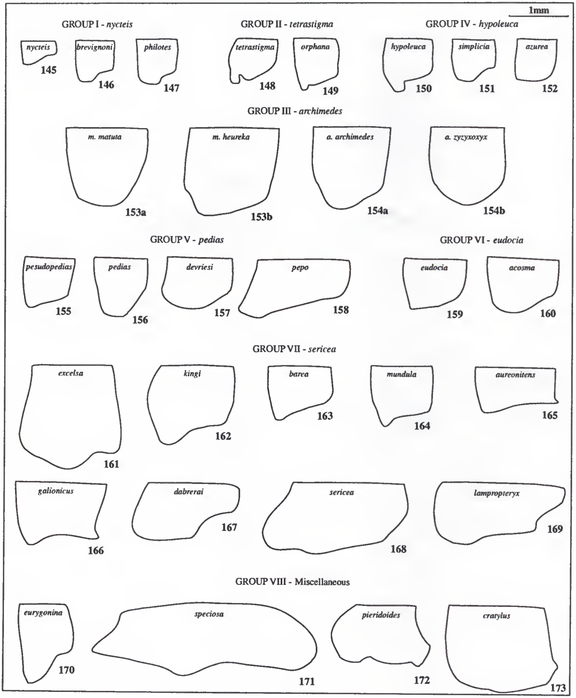
Figs. 122-124. Male genitalia in lateral view (both left and right lateral views for figs. 123-124). Unless otherwise stated, accompanying structures represent the last male sternite in ventral view. See Appendix B for specimen data. **122**. *T. sobrina*. **123**. *T. phaeo*; and aedeagus in ventral view (above right). **124**. *T. theritas*.



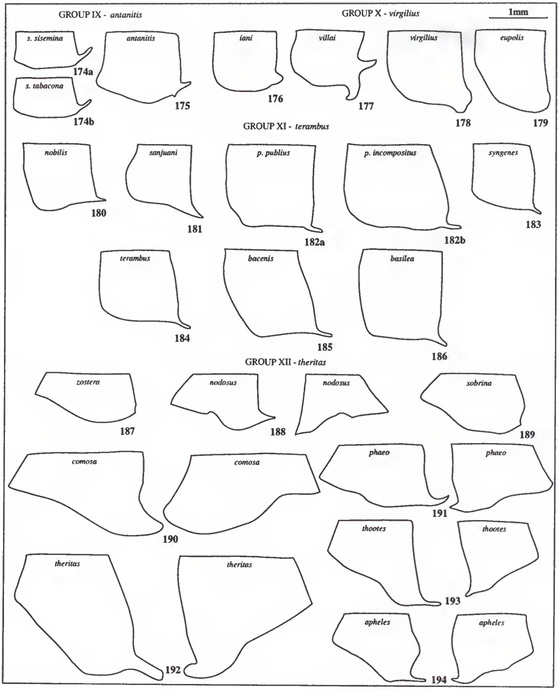
Figs. 125-131. Male genitalia in lateral view (both left and right lateral views for figs. 125-126). Unless otherwise stated, accompanying structures represent the last male sternite in ventral view. See Appendix B for specimen data. **125**. *T. thootes*. **126**. *T. apheles*. **127**. *T. janus*; and subscaphium in ventral view (left). **128**. *T. g. cecropia*. **129**. *T. discus*. **130**. *T. thestias*. **131**. *T. decorata*.



Figs. 132-144. Male genitalia in lateral view. Unless otherwise stated, accompanying structures represent the valvae in dorsal view. See Appendix B for specimen data. **132**. *T. lycaenina*; aedeagus in ventral view (right). **133**. *T. leucanthe*. **134**. *T. amicitiae*. **135**. *T. christiani*. **136**. *T. methemona*. **137**. *T. sticheli*. **138**. *T. busbyi*. **139**. *T. turneri*. **140**. *T. batesi*; genitalia in left and right lateral views: Manicoré, Brazil; lateral view of aedeagus, ventral view of aedeagal tip (below left): Igarapé-Açu, Brazil; lateral view of aedeagus, ventral view of aedeagal tip, dorsal view of expanded androconial setae on right-hand portion of aedeagal tip (below right): nr. Misahualli, Ecuador. **141**. *T. atima*. **142**. *T. foliorum*. **143**. *T. wallacei*; and aedeagus in ventral view (right). **144**. *T. pakitza*; and aedeagus in ventral view (right).



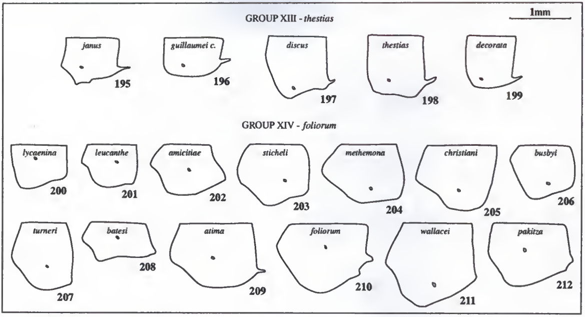
Figs. 145-173. The last (eighth) male abdominal tergite in lateral view. See Appendix B for specimen data.



Figs. 174-194. The last (eighth) male abdominal tergite in lateral view (both left and right lateral views for figs. 188, 190-194). See Appendix B for specimen data.

Figs. 195-212. The last (eighth) male abdominal tergite in lateral view; note small, lightly sclerotised fenestration in each. See Appendix B for specimen data.

Figs. 213-217. Female genitalia in dorsal view. Accompanying structures represent the ostium bursae in ventral view (towards top) and the signa in dorsal view (towards bottom). See Appendix B for specimen data. **213**. *T. nycteis*. **214**. *T. philotes*. **215**. *T. tetrastigma*. **216**. *T. simplicia*. **217**. *T. azurea*.


GROUP XIII - *thestias*
1mm
janus
195
guillaumei c.
196
discus
197
thestias
198
decorata
199
GROUP XIV - *foliorum*
lycaenina
200
leucanthe
201
amicitiae
202
sticheli
203
methemona
204
christiani
205
busbyi
206
turneri
207
batesi
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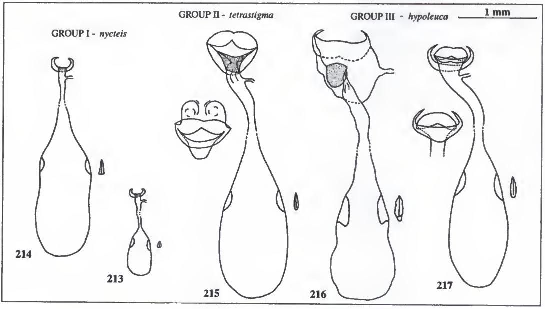
atima
209
foliorum
210
wallacei
211
pakitza
212


GROUP I - *nycteis*
GROUP II - *tetrastigma*
GROUP III - *hypoleuca*
1 mm
214
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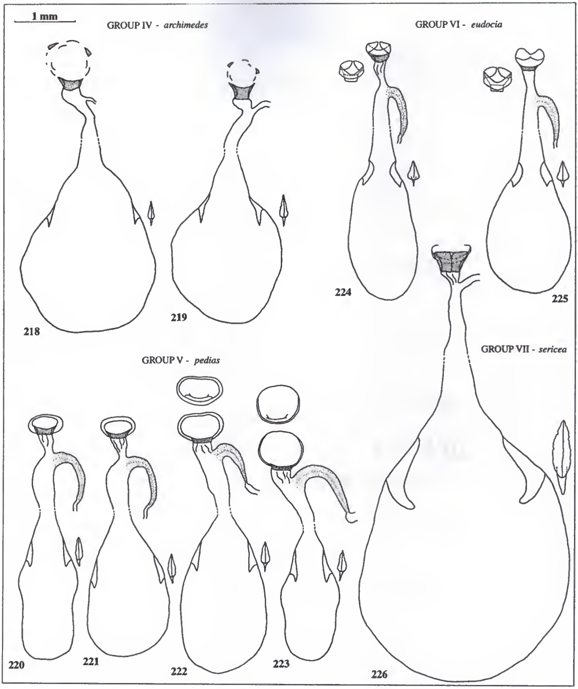
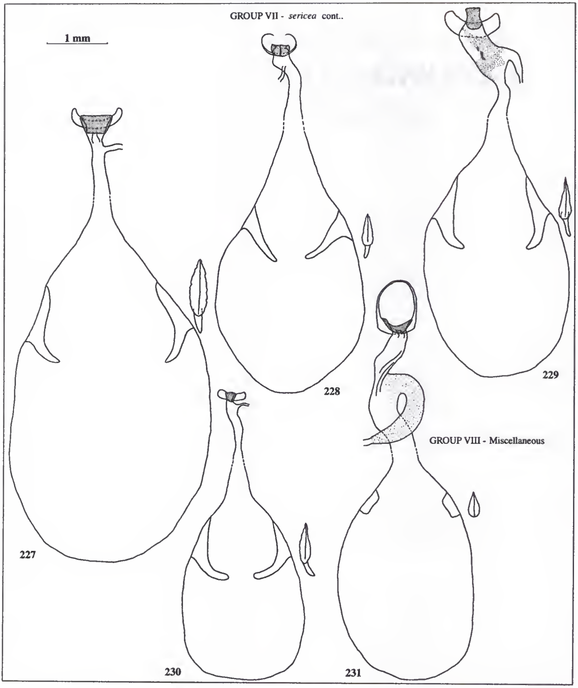
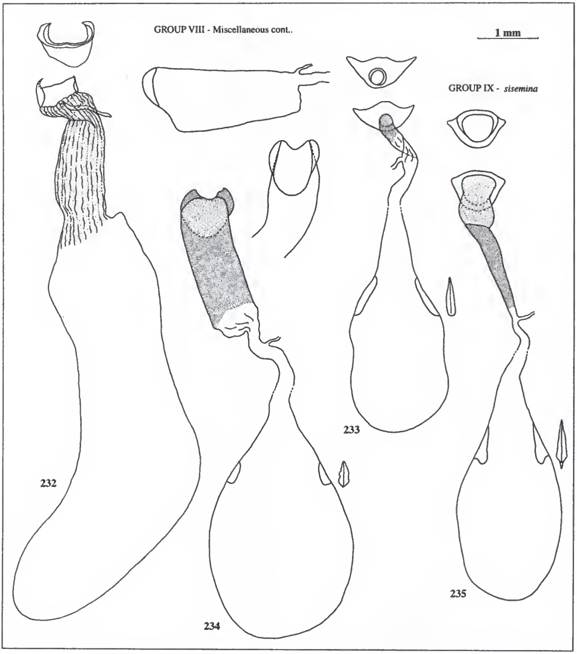


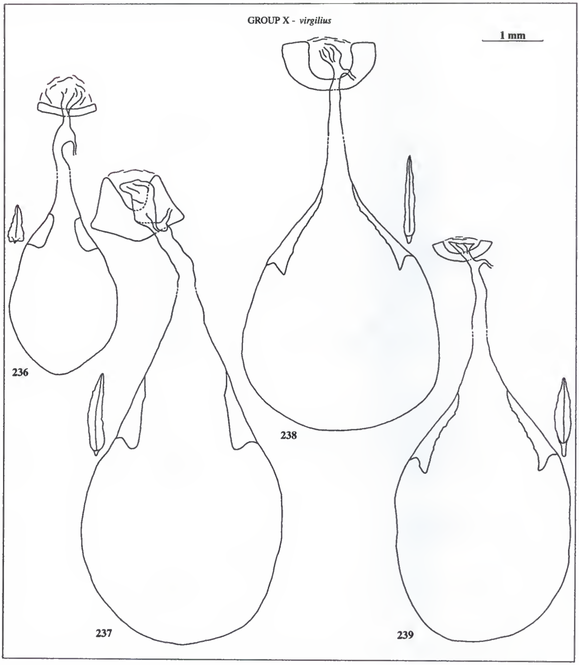
Figs. 218-226. Female genitalia in dorsal view. Accompanying structures represent the ostium bursae in ventral view (towards top) and the signa in dorsal view (towards bottom). See Appendix B for specimen data. **218**. *T. a. archimedes*. **219**. *T. m. matuta*. **220**. *T. pseudopedias* n. sp.. **221**. *T. pedias*. **222**. *T. devriesi*. **223**. *T. pepo*. **224**. *T. eudocia*. **225**. *T. acosma*. **226**. *T. excelsa*.



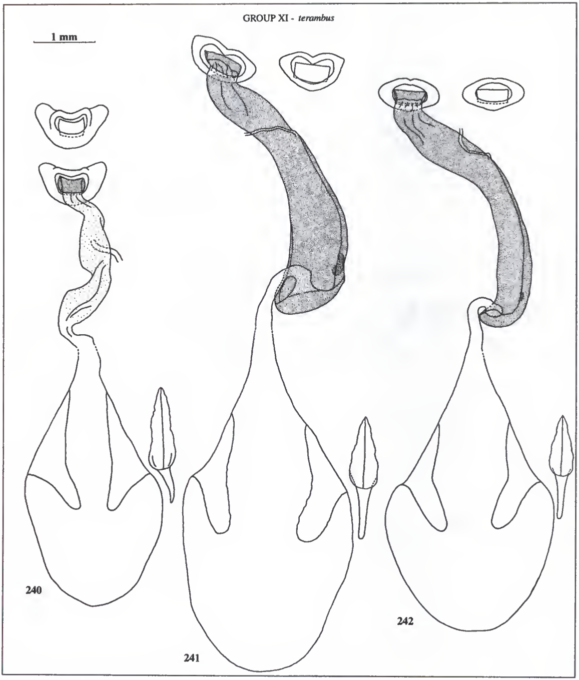
Figs. 227-231. Female genitalia in dorsal view. Accompanying structures represent the signa in dorsal view. See Appendix B for specimen data. **227**. *T. kingi*. **228**. *T. barea*. **229**. *T. mundula*. **230**. *T. galionicus*. **231**. *T. speciosa*.



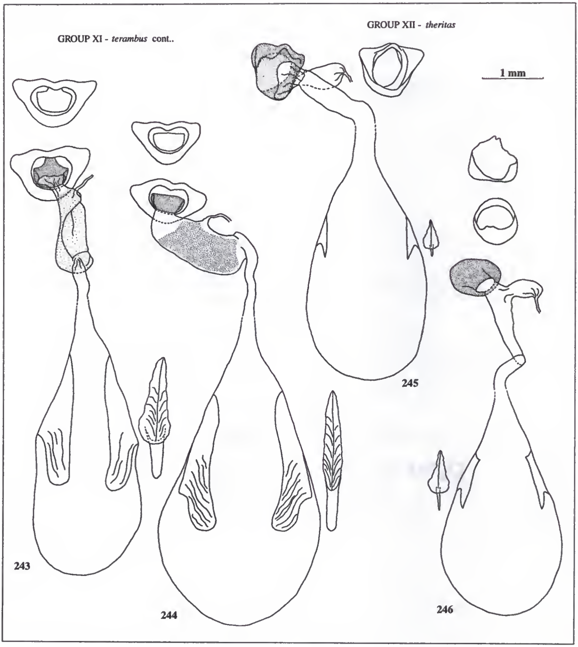
Figs. 232-235. Female genitalia in dorsal view. Unless otherwise stated, accompanying structures represent the ostium bursae in ventral view (towards top) and the signa in dorsal view (towards bottom). See Appendix B for specimen data. **232**. *T. eurygonina*. **233**. *T. pieridoides*. **234**. *T. cratylus*; and lateral view of posterior portion of ductus bursae (at top). **235**. *T. s. sisemina*.



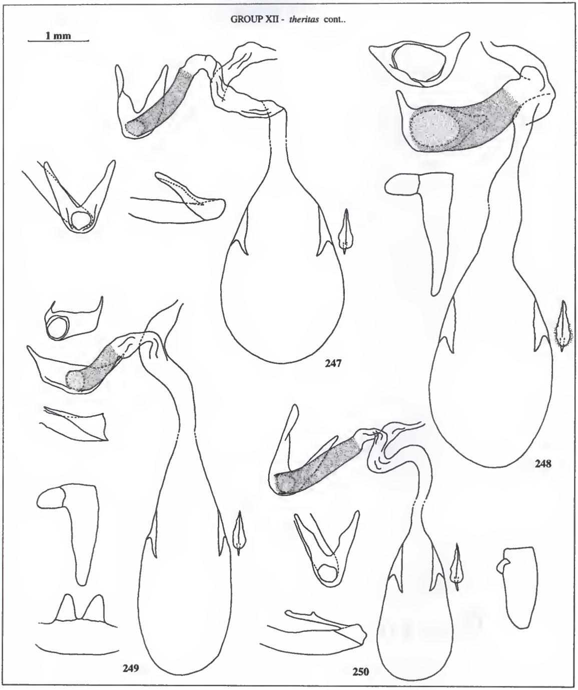
Figs. 236-239. Female genitalia in dorsal view. Accompanying structures represent the signa in dorsal view. See Appendix B for specimen data. **236**. *T. iani*. **237**. *T. villai*. **238**. *T. virgilius*. **239**. *T. eupolis*.



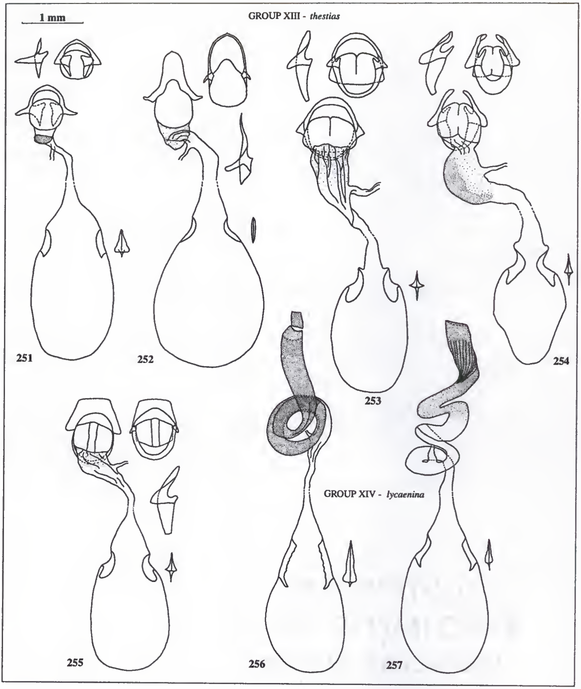
Figs. 240-242. Female genitalia in dorsal view. Accompanying structures represent the ostium bursae in ventral view (towards top) and the signa in dorsal view (towards bottom). See Appendix B for specimen data. **240**. *T. p. publius*. **241**. *T. syngenes*. **242**. *T. terambus*.



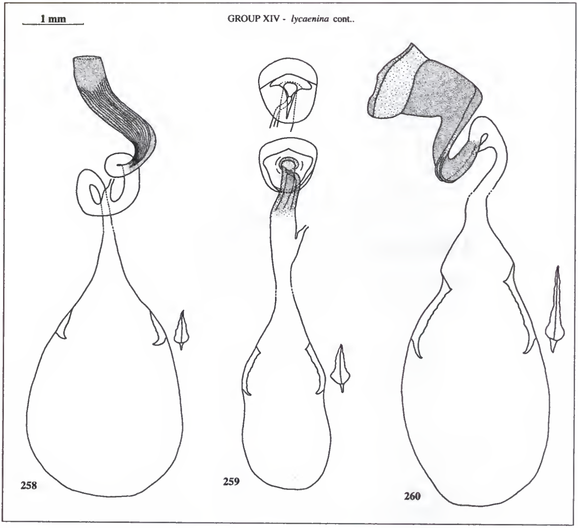
Figs. 243-246. Female genitalia in dorsal view. Unless otherwise stated, accompanying structures represent the ostium bursae in ventral view (towards top) and the signa in dorsal view (towards bottom). See Appendix B for specimen data. **243**. *T. bacenis*. **244**. *T. basilea*. **245**. *T. comosa*. **246**. *T. phaeo*; and dorsal view of ostium bursae (at top).



Figs. 247-250. Female genitalia in dorsal view. Unless otherwise stated, accompanying structures represent the ostium bursae in ventral view (towards top) and the signa in dorsal view (towards bottom). See Appendix B for specimen data. **247.** *T. sobrina*; and ostium bursae and ductus bursae in lateral view (left). **248.** *T. theritas*; and last tergite in lateral view (left). **249.** *T. thootes*; and ostium bursae and ductus bursae in lateral view (upper left); and last tergite in lateral and dorsal view (lower left). **250.***T. apheles*; and ostium bursae and ductus bursae in lateral view (lower left); and last tergite in lateral view (right).

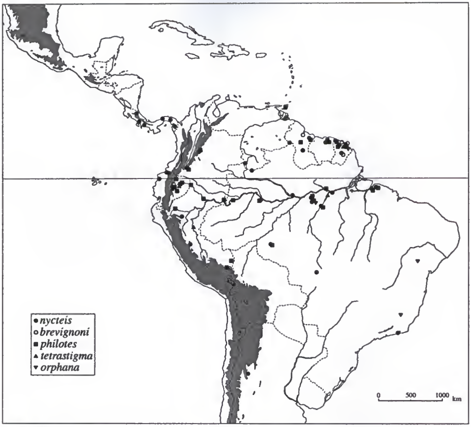


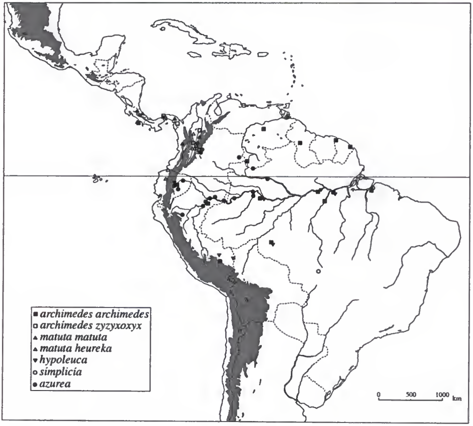
Figs. 251-257. Female genitalia in dorsal view. Accompanying structures represent the ostium bursae in ventral and lateral view (towards top) and the signa in dorsal view (towards bottom). See Appendix B for specimen data. **251**. *T. janus*. **252**. *T. g. guillaumei*. **253**. *T. discus*. **254**. *T. thestias*. **255**. *T. decorata*. **256**. *T. lycaenina*. **257**. *T. leucanthe*.



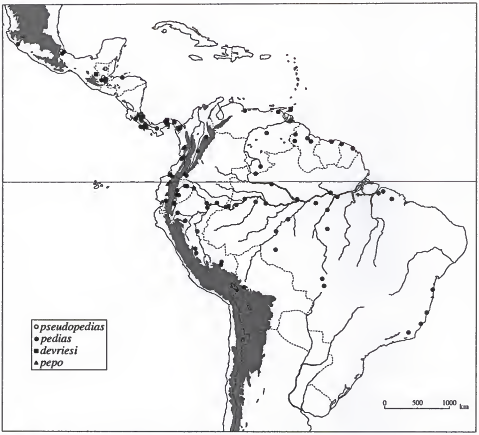
Figs. 258-260. Female genitalia in dorsal view. Unless otherwise stated, accompanying structures represent the signa in dorsal view. See Appendix B for specimen data. **258**. *T. sticheli*. **259**. *T. foliorum*; and ostium bursae in ventral view. **260**. *T. wallacei*.

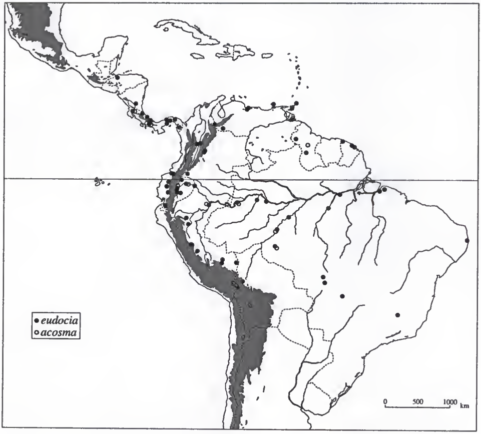
Figs. 261 (above) and 262 (below). Maps of the Neotropics illustrating the distribution of Group I, II (above), III and IV (below) *Theope* species. Shaded areas represent land above 1500 meters.


● nycteis
○ brevignoni
■ philotes
▲ tetrastigma
▼ orphana
0 500 1000 km

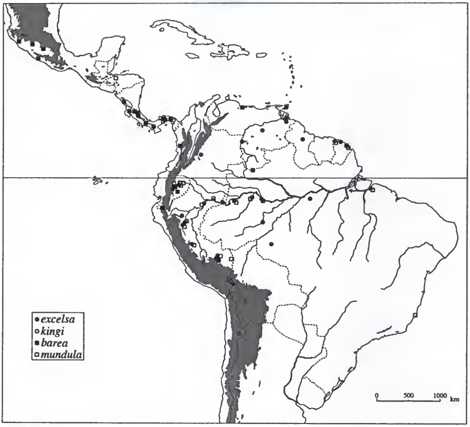

■ archimedes archimedes
□ archimedes zyzyxoxyx
▲ matuta matuta
▲ matuta heureka
▼ hypoleuca
○ simplicia
● azurea
0 500 1000 km

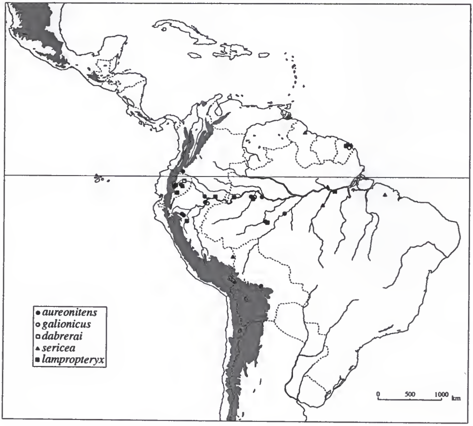
Figs. 263 (above) and 264 (below). Maps of the Neotropics illustrating the distribution of Group V (above) and VI (below) *Theope* species. Shaded areas represent land above 1500 meters.


○ pseudopedias
● pedias
■ devriesi
▲ pepo
0 500 1000 km

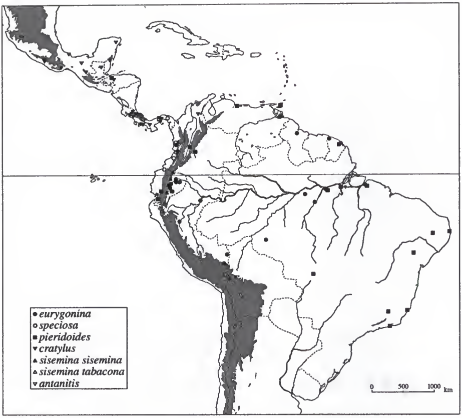

● eudocia
○ acosma
0 500 1000 km

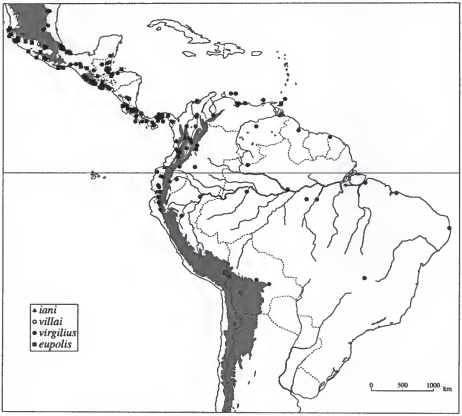
Figs. 265 (above) and 266 (below). Maps of the Neotropics illustrating the distribution of Group VII *Theope* species. Shaded areas represent land above 1500 meters.


● excelsa
○ kingi
■ barea
□ mundula
0 500 1000 km

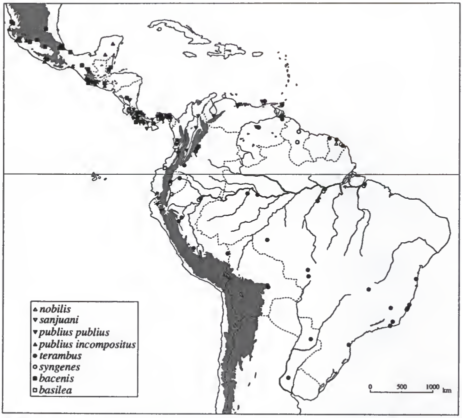

● aureonitens
○ galionicus
□ dabrerai
▲ sericea
■ lampropteryx
0 500 1000 km

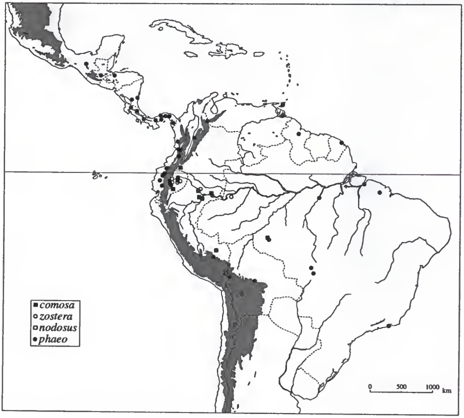
Figs. 267 (above) and 268 (below). Maps of the Neotropics illustrating the distribution of Group VIII, IX (above) and X (below) *Theope* species. Shaded areas represent land above 1500 meters.


● eurygonina
○ speciosa
■ pieridoides
▼ cratylus
▲ sisemina sisemina
△ sisemina tabacona
▽ antanitis
0 500 1000 km

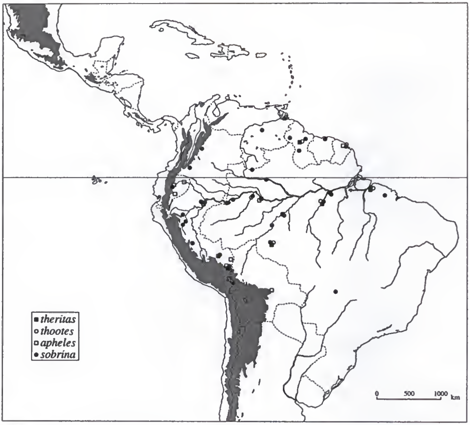

▲ iani
○ villai
● virgilius
■ eupolis
0 500 1000 km

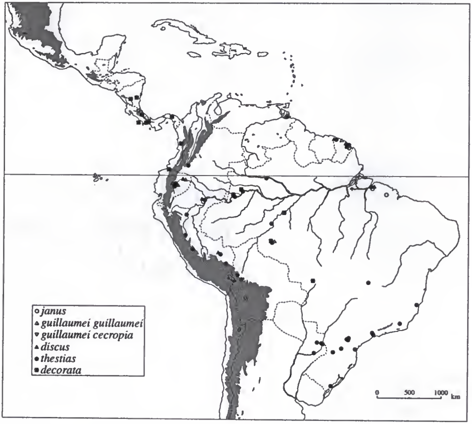
Figs. 269 (above) and 270 (below). Maps of the Neotropics illustrating the distribution of Group XI (above) and XII (partim) (below) *Theope* species. Shaded areas represent land above 1500 meters.


▲ nobilis
▼ sanjuani
▼ publius publius
▲ publius incompositus
● terambus
○ syngenes
■ bacenis
□ basilea
0 500 1000 km

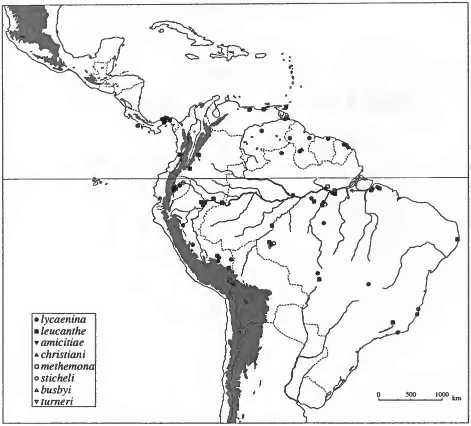

■ comosa
○ zostera
□ nodosus
● phaeo
0 500 1000 km

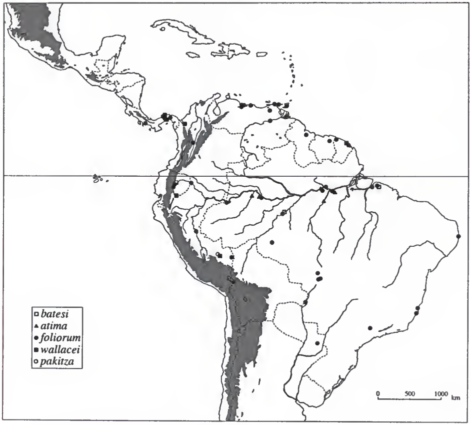
Figs. 271 (above) and 272 (below). Maps of the Neotropics illustrating the distribution of Group XII (partim) (above) and XIII (below) *Theope* species. Shaded areas represent land above 1500 meters.


■ theritas
○ thootes
□ apheles
● sobrina
0
500
1000 km


○ janus
▲ guillaumei guillaumei
▼ guillaumei cecropia
▲ discus
● thestias
■ decorata
0
500
1000 km

Figs. 273 (above) and 274 (below). Maps of the Neotropics illustrating the distribution of Group XIV *Theope* species. Shaded areas represent land above 1500 meters.


● lycaenina
■ leucanthe
▾ amicitiae
▴ christiani
□ methemona
○ sticheli
▴ busbyi
▿ turneri
0
500
1000
km


□ batesi
▴ atima
● foliorum
■ wallacei
○ pakitza
0
500
1000
km

CHAPTER 3
A REVIEW OF THE NEW GENUS *ARCHAEONYMPHA* (LEPIDOPTERA: RIODINIDAE: NYMPHIDIINI)

The sister taxa *drepana* Bates, 1868, and *urichi* Vane-Wright, 1994, have, until recently, been placed in the genus *Theope* (Bridges, 1994), but a morphological cladistic analysis of the tribe Nymphidiini (*sensu* Harvey, 1987) indicates that they do not belong in that genus or any other (Hall, in prep). In order to maintain the monophyly of *Theope*, a new genus, *Archaeonympha* Hall, 1998, was described to include these two species and a third, new species, *smalli* Hall & Harvey, 1998, from Panama (Hall & Harvey, 1998). To evaluate the geographic distribution and abundance of these species, the private collections of G. W. Busby (Boston), R. C. Busby (Boston), and P. J. DeVries (Eugene) as well as the following museums, whose acronyms are used in the text, were examined:

AME	Allyn Museum of Entomology, Florida Museum of Natural History, Sarasota, FL, U.S.A.
AMNH	American Museum of Natural History, New York, NY, U.S.A.
BMNH	Natural History Museum, London, England
FSCA	Florida State Collection of Arthropods, Division of Plant Industry, Gainesville, FL, U.S.A.
MCZ	Museum of Comparative Zoology, Harvard University, Boston, MA, U.S.A.
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.
ZMHU	Zoologische Museum für Naturkunde, Humboldt Universität, Berlin, Germany

Archaeonympha Hall, 1998

Figs. 275-283.

Type species: *Archaeonympha smalli* Hall & Harvey, 1998

Description.- MALE: forewing length 10 to 11 mm. *Wing shape*: distal margin of both wings variably angular, forewing apex variably falcate, distal hindwing margin variably serrate. *Venation* (Fig. 278a): four forewing radial veins, veins Sc and R1 joined for a short distance but not fused. *Dorsal surface*: ground color dark brown; both wings predominantly blue and variably traversed by jagged dark brown discal and postdiscal lines, submarginal dark brown spots on hindwing variably present; fringes brown. *Ventral surface*: ground color a grainy mixture of pale and darker brown scaling; both wings with orange-brown markings forming broken and disjointed basal, mid-discal and postdiscal lines, orange-brown line marks discal cell end of both wings, white distal to apical portion of postdiscal forewing line is variably present; submarginal line of small black spots on both wings lined with white proximally consists of two spots in cell Cu2 and one in cells Cu1 to R5/Sc + R1, slightly darker brown scaling forms indistinct line proximally; thin orange-brown line at distal margin; fringes brown. *Head*: ventral surface of labial palpi gray, dorsal surface brown, second and third segments elongate (Fig. 278b). Eyes bare and brown, margins brown. Frons brown, paler brown at margins. Antennae brown or orange-brown with pale brown at base of each segment; tubular clubs brown or orange-brown, tips pale orange-brown. *Body*: dorsal surface of thorax and abdomen dark brown, ventral surface gray-brown. All legs gray-brown. Tarsus of foreleg unimerous, coxa elongate (Fig. 278c); midleg and hindleg with a tibial spur and a group of spines at inner distal tip of tarsal segments one to four, three further spines along inner distal margin of first tarsal segment (Fig. 278d). *Genitalia* (Figs. 279-280): distal margin of uncus concave; falci small and compact; valvae form an approximate rectangle, with a basal, lateral bulge, a variably sized, rounded lower projection and an upwardly pointed tip with a small bulge below; aedeagus tapers sharply towards tip (*smalli*) or is of even width (*drepana*), tip of vesica contains a double row of small spines (*smalli*) or a jagged sclerotised line (*drepana*); pedicel broad. Eighth tergite has a small triangular point at lower posterior corner. Eighth sternite is a simple rectangle that is weakly indented at posterior margin.

FEMALE: differs externally from male in following ways: forewing length 10 to 15 mm. *Wing shape*: distal margins of both wings less angular, forewing apex never falcate. *Dorsal surface*: ground color of both wings paler brown; blue coloration on both wings a paler lilac, submarginal dark brown spots on hindwing always present. *Ventral surface*: ground color slightly paler. *Head*: second palpal segment slightly more elongate (Fig. 278e). Inside edge of antennae bare brown. *Body*: foreleg with a group of spines at inner distal tip of tibia and tarsal segments two to four (Fig. 278f). *Genitalia* (Figs. 281-283): corpus bursae variably constricted at or below signae, signae form pointed invaginations that are inwardly curved (*smalli*) or sinuate (*drepana* and *urichi*), triangular (*smalli*) or more ovate (*drepana* and *urichi*) at base; ductus bursae hardened or sclerotised and bulbous at posterior end with small areas of heavy sclerotization at margin, a variably elongate, hollow, sclerotised structure that is medially divided in posterior half positioned opposite opening of ductus seminalis; ostium bursae forms a roundly triangular sclerotised ring; region between ostium bursae and eighth tergite partially sclerotised with a pair of small indentations. Eighth tergite has a heavily sclerotised disc at dorsal posterior corner.

Systematic position.- *Archaeonympha* species have been treated in both *Comphotis* Stichel, 1910, because of their small size and similarly patterned ventral surface, and *Theope*, because of their blue dorsal surface, but their true systematic position has been uncertain (Hall & Willmott, 1996b). The ventral position of the spiracle on male abdominal segment three of *Archaeonympha* species places them in the tribe Nymphidiini (*sensu* Harvey, 1987) and they are thus not closely related to *Comphotis* species, which lack the synapomorphic characters of any existing tribe and can only be placed in the *incertae sedis* section (four forewing radial veins) of Harvey (1987); *Comphotis* species also have brown, orange or red dorsal coloration with a slightly different and diagnostic ventral pattern (Hall & Willmott, 1996b).

A comprehensive morphological cladistic analysis of the Nymphidiini, (*sensu* Harvey, 1987) based on over 85 percent of species from all described genera, indicates that while *Archaeonympha* species are closely related to those of *Theope* they do not together form a monophyletic clade (Hall, in prep). *Archaeonympha* species appear to be most closely related to the taxon *senta* Hewitson, [1853], which is currently misplaced in the polyphyletic genus *Adelotypa* Warren, 1895, and all four species occupy a basal position in the tribe (Hall, in prep). Although the ventral patterning of *Archaeonympha* species and *senta* is very similar and unique to these species, the differences in the remaining pattern elements, and male and female genitalic morphology are so gross as to indicate that at least one of these groups has undergone substantial anagenesis. For this reason, and uncertainty concerning the monophyly of *Archaeonympha* + *senta*, *senta* is not included in *Archaeonympha*, and indeed it requires its own monotypic genus (Hall, in prep.).

Diagnosis.- *Archaeonympha* species are superficially readily recognisable by their small size, angular wing shape, blue dorsal coloration that is typically divided by brown transverse lines, and orange-brown ventral patterning with tiny, black, white-encircled submarginal spots around both wings. The lack of a sclerotised transtilla at the tip of the valvae of the male genitalia distinguishes *Archaeonympha* from most nymphidiine genera and the lack of a dorsal sclerotised invagination to the eighth male abdominal sternite distinguishes *Archaeonympha* from *Theope* and its closest relatives. The monophyly of *Archaeonympha* is best supported by the following unique synapomorphy of the female genitalia: the presence in the ductus bursae, opposite the opening of the ductus seminalis, of a variably elongate, hollow, sclerotised structure that is medially divided in its posterior half.

Biology.- Nothing is known about the biology of any species in the genus and all are very rare in collections. Of the examined riodinid collections listed above, only the AME, BMNH, USNM and ZMHU contain *Archaeonympha* specimens.

Distribution.- *Archaeonympha* species are known to occur in only a few disjunct localities in Nicaragua, Panama, Brazil, Peru and Trinidad (Fig. 284), but the true range of the genus undoubtedly encompasses all intervening areas where there is suitable habitat. Panama is the only country in which two *Archaeonympha* species are known to occur.

Archaeonympha smalli Hall & Harvey, 1998

Figs. 275a-d; 278a-f; 279, 281.

Archaeonympha smalli Hall & Harvey, 1998. *Trop. Lepid.*, 9(Suppl. 1): 38, figs. 1a-d. **TL**: Cocoli, Panama. Holotype male and allotype female USNM [Examined].

Identification and Taxonomy: Both sexes of *A. smalli* differ from *A. drepana* and *A. urichi* (which is only known from the female) by having a more rounded wing shape, without a falcate forewing apex and an undulating margin to an angular hindwing, and a paler, more uniform ventral ground color with more contrasted orange-brown macules. The male of *A. smalli* additionally differs from that of *A. drepana* by having slightly darker blue dorsal coloration that is reduced to the base of the forewing (especially in Panamanian specimens), no transverse brown lines on either dorsal wing and in the genitalia by having a prominent lower projection on the valvae, a pointed aedeagal tip and two rows of internal aedeagal spines instead of a continuous, jagged sclerotised line. The female of *A. smalli* additionally differs from those of both species by having paler lilac blue dorsal coloration and in the genitalia by having a less medially constricted corpus bursae, a less elongate base to the signae, a hardened although not sclerotised posterior portion to the ductus bursae and a more elongate sclerotised structure in the ductus bursae that is closer to the ostium bursae.

Biology: Nothing is known about the biology of this very rare species, although collection data indicate that it is present year round and most common in the months December to March.

Distribution: Although currently known only from Nicaragua and Panama, it clearly occurs in Costa Rica and will probably eventually be found to range into the Chocó region of west Colombia and west Ecuador.

Specimens Examined: 7M 2F

NICARAGUA: *Atlántico Sur*, Bluefields (Oct, Dec) 1M, 2F AME. **PANAMA**: *Canal Zone*, Cocoli (Jan-Mar, Oct) 7M, 3F USNM; *Darién*, Río Tuquesa (Jul) 1F USNM.

Archaeonympha drepana (Bates, 1868), **n. comb.**

Figs. 276a-d; 280, 282.

Theope drepana Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9: 409. **TL**: Ega, W. Brazil. Syntype male and female BMNH [Examined] (Fig. 3.2a,b).

= ***Comphotis sinuata*** Stichel, 1925. *Z. wiss. InsektBiol.* 20: 53. **TL**: Manicoré, C. Brazil. Holotype male ZMHU [Examined].

Identification and taxonomy: Average FW length 10mm.

The sexes are similar but the female has a less falcate forewing, slightly reduced blue postdiscally on the dorsal forewing, and more prominent transverse brown lines through the blue on both dorsal wing surfaces. *A. drepana* differs from its closest relative *A. urichi* by its considerably smaller size, and by having a more distally positioned postdiscal line on both ventral wings and a more prominent whitish square in the apex of the ventral forewing. The female genitalia of the two species do not differ significantly. The type of *sinuata* differs very littele from that of *drepana* and was synonymised with it by Hall & Willmott (1996b).

Biology: Nothing is known of the biology of this very rare species and most museum specimens were collected by H. W. Bates in the 1850's.

Distribution: Specimens of *A. drepana* have been examined only from the disjunct areas of central-western Brazil and the Tambopata reserve of south-east Peru (as listed by Lamas (1994)), and the true extent of its Amazonian range is uncertain.

Specimens Examined: 7M 2F

PERU: *Madre de Dios*, Reserva Tambopata, 12°50'S 69°17'W (Oct) 1M USNM(?). **BRAZIL**: *Amazonas*, Ega 3M, 1F BMNH; Manicoré (Dec) 1M ZMHU; Amazon 1M BMNH. Undetermined locality data 1F ZMHU. No locality data 1M BMNH.

Archaeonympha urichi (Vane-Wright, 1994), **n. comb.**

Figs. 277a,b; 283.

Theope urichi Vane-Wright, 1994. In: B. D'Abrera, *Butts. Neotropical Region, Part VI*: 1002, figs. **TL**: Sangre Grande, Trinidad. Holotype female in coll. F. C. Urich, Sangre Grande, Trinidad; type illustration [Examined].

Identification and taxonomy: Average FW length 15mm.

A. urichi is the only *Archaeonympha* species for which the male is unknown. Female *A. urichi* consistently differs from that of *A. drepana* only in its considerably larger size and by having a slightly proximally displaced postdiscal line of chestnut-brown spots on both ventral wing surfaces. These two characters unite the single illustrated Panamanian specimen with the nominotypical Trinidadian ones (figured in D'Abrera, 1994), although the latter have greatly reduced blue on both dorsal wing surfaces. It remains to be seen whether these specimens really are conspecific and whether *A. urichi* is actually a different species to *A. drepana*, especially in light of the fact that the female genitalia of the two species do not differ. More material, including males, is needed from intervening areas to answer these questions.

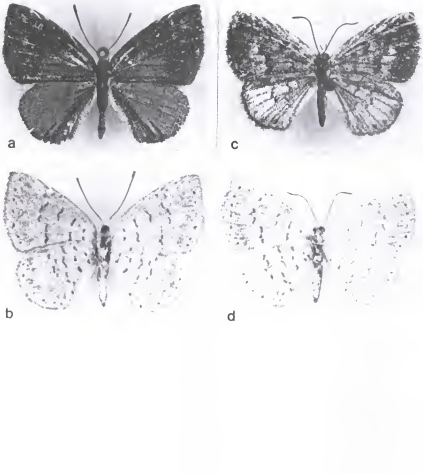
Biology: F. C. Urich (pers. comm. to JPWH) reports that both female types were collected flying across the lawn on his forested estate.

Distribution: *T. urichi* is only known with certainty from the two female types collected by the eponymous F. C. Urich on Sans Souci Estate, Sangre Grande, Trinidad. A female from Panama, which is tentatively illustrated here as belonging to this species, suggests a broader northern South American range.

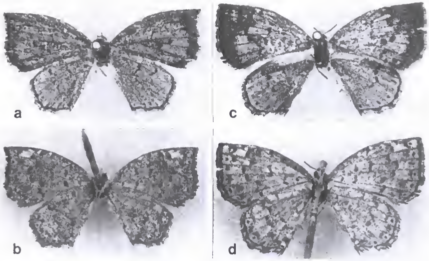
Specimens Examined: 1F

PANAMA: *Panamá*, N. of El Llano (330m) (Oct) 1F USNM.

Fig. 275. *Archaeonympha smalli* Hall & Harvey, 1998, holotype male: a) dorsal surface; b) ventral surface. Allotype female c) dorsal surface; d) ventral surface.


a
c
b
d

Figs. 276-277. **276 (above).** *Archaeonympha drepana* (Bates, 1868). Syntype male, Ega, Brazil: a) dorsal surface; b) ventral surface. Syntype female, Ega, Brazil: c) dorsal surface; d) ventral surface. **277 (below).** *Archaeonympha urichi* (Vane-Wright, 1994). Female, El Llano, Panama: a) dorsal surface; b) ventral surface.


a
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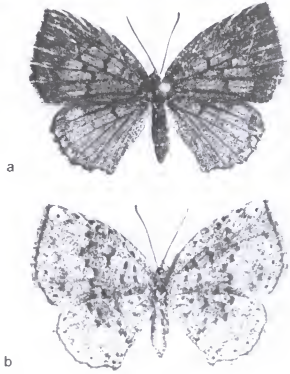
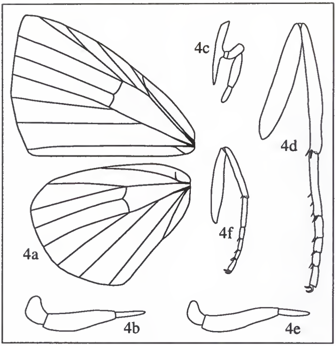

a
b

Figs. 278a-f. Morphology. **278.** *Archaeonympha smalli*, male: a) venation; b) palpus; c) foreleg; d) hindleg. Female: e) palpus; f) foreleg.

Figs. 279-283. Male genitalia: **279.** *Archaeonympha smalli.* **280.** *Archaeonympha drepana.* Female genitalia: **281.** *Archaeonympha smalli.* **282.** *Archaeonympha drepana.* **283.** *Archaeonympha urichi.*


4c
4d
4f
4a
4b
4e

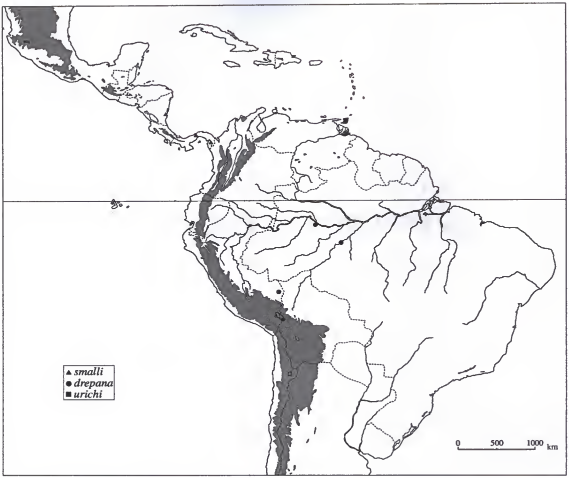


Fig. 284. A map of Central and South America showing the distribution of *Archaeonympha* species.

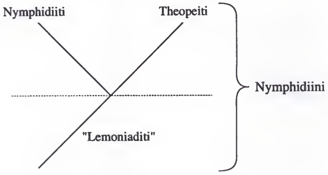
CHAPTER 4
A PHYLOGENY OF THE NEOTROPICAL RIODINID SUBTRIBE THEOPEITI (LEPIDOPTERA: RIODINIDAE: NYMPHIDIINI)

Introduction

Once the subtribe Theopeiti has been revised at the species level, it becomes possible to generate a comprehensive phylogeny for the group. The purpose of doing so, using the largest morphological data set ever compiled for the Riodinidae, is to begin the process of recognising monophyletic groups in the family and elucidating phylogenetic relationships between them to create a natural, "modern" generic classification. The evolution of any number of character traits may then also be traced on the cladogram. No such phylogeny has yet been created for any large riodinid group and the cladistic method has only been applied to the family in recent years (DeVries, 1997; Hall, 1998b; Penz & DeVries, in press).

As outlined earlier, the absence of sclerotised tissue joining the distal portion of the valvae of the male genitalia (often termed a transtilla) defines the monophyletic nymphidiine subtribe Theopeiti. Further characteristic male genitalic traits include the lack of a vinculum dorsally, at the anterior edge of the tegumen, and the lack of a saccus. Figure 285 illustrates the phylogenetic relationships between the three nymphidiine subtribes, as outlined in Chapter 1.

Fig. 285. A preliminary higher classification for the riodinid tribe Nymphidiini. The monophyletic clades above the dotted line together constitute the Nymphidiini of Harvey (1987), and the paraphyletic stem below the line constitutes the Lemoniadini (as Lemoniini) of Harvey (1987).



Methods

Taxa Studied

There has recently been an explosion of interest in the effect of taxon sampling on the resulting phylogenetic hypothesis, with a general consensus that judicious addition of taxa is often likely to give better resolution to the cladogram (Lecointre *et al.*, 1993; Hillis, 1996, 1998), particularly through the splitting up of long branches (Hendy & Penny, 1989; Graybeal, 1998), and it will certainly lead to the useful elimination of previously unwittingly used spurious characters and character states. Of course, even the omission of as yet undiscovered species and extinct species (see DeVries & Poinar (1997) for an illustration and discussion of a fossilised putative *Theope* larva) will adversely affect the accuracy of the phylogenetic hypothesis, but the extant taxon saturation approach is the best available and the one adopted here as the surest method of elucidating the monophyly of genera and their phylogenetic relationships. Thus all 75 species (see Figs. 286 and 287 for representatives) identified as belonging to the subtribe Theopeiti are incorporated into this analysis. These include all 68 species of *Theope*, the largest genus in the tribe and also the third largest in the entire family after the genera *Euselasia* Hübner and *Mesosemia* Hübner (Bridges, 1994; Hall, unpubl. data), for which capture localities and institutional locations of all specimens examined (4241) and dissected (240) are listed in the revision of that genus (see Chapter 2), and an additional 7 species; 3 of these belong to *Archaeonympha* (see Hall & Harvey, 1998), and the remainder are currently erroneously treated in the genera *Adelotypa* Warren, *Calociasma* Stichel, and *Pandemos* Hübner (Bridges, 1994). The capture locality and institutional location of specimens dissected for these species are listed in Table 8; a list of all *Archaeonympha* specimens examined is given in Hall & Harvey (1998).

Table 8. A list of study taxa outside of the genus *Theope* (see Appendix 3 for list of *Theope*) and dissections examined. Note that the male of *Archaeonympha urichi* and the female of "*Calociasma*" sp. n. are unknown. The following collection acronyms are used: FSCA - Florida State Collection of Arthropods, Division of Plant Industry, Gainesville, FL, USA; JHKW - Collection of Jason P. W. Hall and Keith R. Willmott, Gainesville, FL, USA; USNM - National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; ZMHU - Zoologische Museum für Naturkunde, Humboldt Universität, Berlin, Germany.

Taxa	Dissections examined
Thisbe irenea (Stoll, [1780]) [outgroup]	1 male: Ecuador, Napo, Pimpilala (JHKW); 1 female: Ecuador, Manabí, Ayampe (JHKW)
"*Adelotypa*" *senta* (Hewitson, [1853])	2 males: Brazil, Rondônia, nr. Cacaulandia (FSCA); 1 female: Brazil, Rondônia, nr. Cacaulandia (FSCA); 1 female: Ecuador, Napo, nr. Misahualli (JHKW)
Archaeonympha smalli Hall & Harvey, 1998	2 males: Panama, Canal Zone, Cocoli (USNM); 1 female: Panama, Canal Zone, Cocoli (USNM)
Archaeonympha drepana (Bates, 1868)	1 male: Brazil, Amazonas, Manicoré (ZMHU); 1 female: unknown locality data (ZMHU)
Archaeonympha urichi (Vane-Wright, 1994)	1 female: Panama, Panamá, nr. El Llano (USNM)
"*Calociasma*" *lilina* (Butler, 1870)	1 male: Panama, Canal Zone, Paraiso (FSCA); 1 female: Mexico, San Luis Potosí, El Salto Falls (FSCA)
"*Calociasma*" sp. n.	1 male: Panama, Canal Zone (USNM)
"*Pandemos*" *godmanii* Dewitz, 1877	1 male: Mexico, Veracruz, Paso San Juan (USNM); 1 female: Mexico, Veracruz, Rinconada (USNM)

Fig. 286. Sample of study taxa representing members from all clades of generic worth (clades A-E in Fig. 288 and marked here) and all clades of species group worth within the largest genus *Theope* (clades 1-13 in Fig. 288 and marked here). Wing shape, dorsal wing pattern and dorsal abdominal characters 2-11 and 31-32 from Table 9 are illustrated here. All specimens are males unless otherwise stated. **A**: *Thisbe irenea* [outgroup taxon]; **B**: "*Adelotypa*" *senta* [A]; **C**: *Archaeonympha smalli* [B]; **D**: *Archaeonympha urichi* [B]; **E**: "*Calociasma*" *lilina* [C]; **F**: "*Pandemos*" *godmanii* [D]; **G**: *Theope brevignoni* [E,1]; **H**: *Theope tetrastigma* [2]; **I**: *Theope hypoleuca* [3]; **J**: *Theope matuta heureka* [4]; **K**: *Theope pepo* [5]; **L**: *Theope pepo* (female) [5]; **M**: *Theope acosma* [6]; **N**: *Theope aureonitens* [6]; **O**: *Theope sisemina sisemina* [7]; **P**: *Theope virgilius* [8]; **Q**: *Theope virgilius* (female) [9]; **R**: *Theope basilea* [10]; **S**: *Theope publius publius* [10]; **T**: *Theope sobrina* [11]; **U**: *Theope sobrina* (female) [11]; **V**: *Theope decorata* [12]; **W**: *Theope decorata* (female) [12]; **X**: *Theope lycaenina* [13]; **Y**: *Theope wallacei* [13].

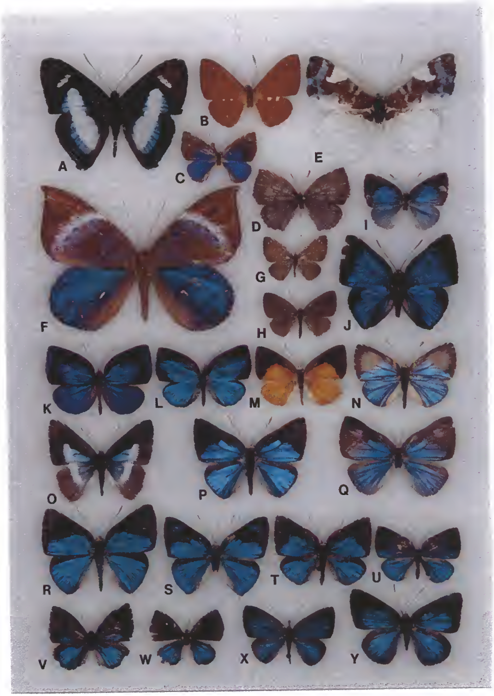

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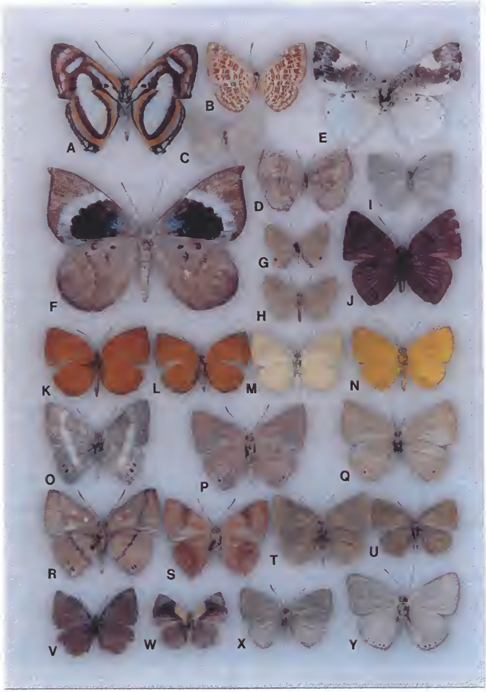
Fig. 287. Same sample of study taxa illustrated in Fig. 286, illustrating ventral wing pattern and ventral abdominal characters 12-30 and 33 from Table 9.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Morphology

The phylogenetic analyses in this paper are based largely on characters from the internal and external morphology of adults of both sexes, gleaned from specimens collected by myself in Ecuador and from those in a large number (14) of institutions and private collections in Europe, North America and South America (see Chapter 2). Early stage characters of larvae and pupae would undoubtedly provide additional phylogenetic information, as they have done in several other cladistic studies of Lepidoptera (Kitching, 1985; Brown & Freitas, 1994; Miller, 1996; Parsons, 1996), but early stage material is only available for 9 of the study species here (8 *Theope* species and "*Adelotypa*" *senta* (Guppy, 1904; Harvey, 1987; DeVries *et al.*, 1994; DeVries, 1997)), an insufficient 12 percent of the in-group. However, the loss may not be too great, since it is widely hypothesised that larval traits evolve more slowly than those of adults (e.g. Alexander, 1990), and thus early stage characters would be expected to provide the most phylogenetic resolution at levels higher than those treated here, such as the family and subfamily level. This has actually been demonstrated to be the case in notodontid moths (Miller, 1991, 1992, 1996).

Dissections were performed using standard techniques, after having placed abdomens in hot 10 percent potassium hydroxide (KOH) for 10-20 minutes, and the resulting material was stored in glycerol after examination. All characters were scored using light microscopy but a few were also examined with a Hitachi S4000 digital scannning electron microscope (SEM), by rinsing in water and air drying material that was stored in glycerol and mounting it on stubs using carbon tape. The terminolgy for male and female genital and abdominal structures generally follows Klots (1956) and Eliot (1973), while nomenclature for venation follows Comstock & Needham (1918).

Cladistic Analyses

The character matrix consists of 104 characters, of which 67 are binary and 37 are multistate. Autapomorphies (given in Chapter 2 for *Theope* species) are omitted since they are phylogenetically uninformative. Maximum parsimony analyses were implemented through a heuristic search in PAUP 4.0 (Swofford, 1999) using TBR branch-swapping, in which all characters were equally weighted and unordered. Therefore no *a priori* assumptions have been made about the relative importance of characters or the evolutionary history of their component states. *Thisbe irenea* was designated as the outgroup because, by virtue of having a dorsally positioned spiracle on male abdominal segment three, it can be placed outside of the Nymphidiiti + Theopeiti, in the Lemoniaditi, yet of the 8 (out of 10) genera of the Lemoniaditi examined, its genital morphology was most similar to that of the in-group, suggesting it is a derived member of that subtribe. *A posteriori* reweighting, in the form of successive approximations weighting (SAW) (Farris, 1969; Carpenter, 1988), was implemented using the rescaled consistency index of each character, to choose among equally parsimonious trees; SAW is also resilient to the bias associated with initial seed tree choice (Naylor, 1992). Branch support was estimated by means of 1000 bootstrap replicates (Felsenstein, 1985). Character evolution was studied using MacClade 3.01 (Maddison & Maddison, 1992).

Results

Cladograms

A total of 104 characters were identified (Table 9), including 1 behavioral ecological character, 29 from wing shape and pattern, 20 from the male abdomen, 33 from male genitalia and 21 from female genitalia. The data matrix appears in Appendix C. The initial cladistic analysis of this data set generated 120,323 most parsimonious trees (MPTs), a number that represents a ceiling imposed by computer memory rather than a complete set of MPTs, and one that required almost 3 days of computing time to produce on a Macintosh G3. The very high initial number of MPTs is noteworthy but in this particular case is probably due in large part to the high percentage (28%) of missing female genitalic data (the females of many species still remain unknown), and when female genitalic characters are omitted only 39,496 initial MPTs are generated. This number is itself somewhat high, but not surprisingly so given the exclusive use of unordered characters and the large number of taxa included in the analysis, and, despite a common misconception to the contrary, a high number of MPTs is clearly not indicative of low phylogenetic content in the data set (e.g. see Naylor, 1992).

Using Carcharhiniform sharks as his study group, Naylor (1992) experimentally demonstrated that consensus trees based on small sub-samples of the total number of trees yielded very similar topologies to a consensus tree for the total (i.e. the phylogenetic signal is highly similar throughout the course of branch swapping). Since my data corroborate his findings, the strict consenus of 1000 MPTs giving the same topology as the strict consensus of all 120,323 MPTs, I interrupted the heuristic search in subsequent

Table 9. A list of characters employed in the cladistic analysis of the Theopeiti. Unless otherwise stated, taxa for which a character is inapplicable are coded in two different ways: in cases where the states of a character are based on an apomorphic state from a previous character they are coded with a "0" and where the states of a character are based on a plesiomorphic state from a previous character they are coded with a "?". The Consistency Index (CI), Retention Index (RI), and references to figures are given for each character.

Behavioural ecology:

1. Adults rest with wings outspread **[0]**; closed over the body **[1]**. CI=1; RI=1. NOTE: Character states are applied largely on basis of my own field work but in a few instances information has been received from C. Brévignon, J.-Y. Gallard, P. DeVries and M. Cock (pers. comm.).

Wing shape:

2. Base of forewing costa is straight or mildly arched (e.g. Fig. 286H) **[0]**; pronouncedly arched (Fig. 286T) **[1]**. CI=0.5; RI=0.88.

3. A serrate distal hindwing margin is absent **[0]**; present (Fig. 286D) **[1]**. CI=I; RI=1.

4. A bulbously pronounced anal fold is absent **[0]**; present (Fig. 286V) **[1]**. CI=0.5; RI=0.67.

Wing pattern:

5. Dorsal surface of male has blue and/or white scaling (e.g. Fig. 286J) **[0]**; patterned orange scaling (Fig. 286B) **[1]**; uniform orange scaling (Fig. 286M) **[2]**; only brown scaling (e.g. Fig. 286H) **[3]**. CI=0.75; RI=0.83.

6. A white triangle at middle of dorsal forewing costa is absent **[0]**; present (Fig. 286E) **[1]**. CI=1; RI=1.

7. Contrasted area of postdiscal pale brown scales on dorsal forewing of males is absent **[0]**; present (e.g. Fig. 286N) **[1]**. CI=0.25; RI=0.7. See SEM illustration of character state [1] in Chapter 2 (Fig. 3).

8. Costal area of contrasted pale brown scales on dorsal hindwing of males is absent **[0]**; present (Fig. 286T) **[1]**. CI=0.5; RI=0.8. See SEM illustration of character state [1] in Chapter 2 (Fig. 3).

9. An isolated subapical blue patch on dorsal forewing of females is absent (e.g. Fig. 286K) **[0]**; present (Fig. 286Q) **[1]**. CI=0.33; RI=0.67.

10. An elongate postdiscal blue extension in cells M3 and M2 only on dorsal forewing of females is absent (e.g. Fig. 286W) **[0]**; present (Fig. 286U) **[1]**. CI=1; RI=1.

11. An elongate postdiscal blue extension that includes cell Cu1 on dorsal forewing of females is absent (e.g. Fig. 286W) **[0]**; present (Fig. 286L) **[1]**. CI=0.5; RI=0.67.

12. Ventral ground colour of male is predominantly various shades of white, cream or brown (e.g. Fig. 287H) **[0]**; entirely shades of yellow (e.g. Fig. 287N) **[1]**. CI=0.33; RI=0.88.

13. If ventral ground colour of male is a shade of yellow (I2:I), it is matte yellow (Fig. 287M) **[1]**; chrome yellow (Fig. 287N) **[2]**; orange (Fig. 287K) **[3]**. CI=0.6; RI=0.86.

14. Contrasted darker scaling at distal margins of both ventral wing surfaces is absent **[0]**; present (Fig. 287K) **[1]**. CI=1; RI=1.

15. Blue or purple iridescence on ventral surface is absent **[0]**; present (Fig. 287V) **[1]**. CI=1; RI=1.

16. Prominent yellow scaling at base only of ventral forewing is absent **[0]**; present (Fig. 287V) **[1]**. CI=1; RI=1.

17. If prominent yellow scaling at base of ventral forewing only is present (16:1), it is of same extent in both sexes **[1]**; of greater extent in females (Figs. 287V,W) **[2]**. CI=1; RI=1.

18. Red scaling at base of ventral forewing is absent **[0]**; present (Fig. 287J) **[1]**. CI=1; RI=1.

19. Fine scaled yellow banding ("ripple pattern") on ventral surface is absent **[0]**; present (Fig. 287G) **[1]**. CI=I; RI=I.

20. Two spots at base of cell 1A+2A on ventral forewing are present (e.g. Fig. 287C) **[0]**; absent (e.g. Fig. 287H) **[1]**. CI=1; RI=1.

21. White spot in middle of discal cell of ventral forewing is absent **[0]**; present (Fig. 287R) **[1]**. CI=1; RI=1.

22. A postdiscal line of disjointed spots on ventral forewing is absent **[0]**; present (Fig. 287C) **[1]**. CI=1; RI=1.

23. A medial white band on both ventral wing surfaces is absent **[0]**; present (Fig. 287O) **[1]**. CI=1; RI=I.

24. A single dark brown transverse band on ventral forewing is absent **[0]**; present (e.g. Fig. 287R) **[1]**. CI=I; RI=I.

25. If a single dark brown transverse band on ventral forewing is present (24:1), it originates from approximately the mid-point of the costa (Fig. 287S) **[1]**; near the apex (Fig. 287R) **[2]**. CI=I; RI=1.

26. Thin, contrasted yellow line at distal margin of both ventral wing sufaces is absent **[0]**; present (e.g. Fig. 287H) **[1]**. CI=I; RI=1.

27. Black submarginal spots on ventral surface are present (e.g. Fig. 287H) **[0]**; absent (e.g. Fig. 287N) **[1]**. CI=0.13; RI=0.75. NOTE: Character state (0) is applied to a taxon if either sex or any population exhibit such spots.

28. If ventral submarginal spots are present (27:0), they are evenly distributed on forewing (e.g. Fig. 287H) **[0]**; restricted to apex on forewing (Fig. 287G) **[1]**. CI=0.5; RI=0.67.

29. If ventral submarginal spots are present (27:0), they are approximately of even size on hindwing (e.g. Fig. 287H) **[0]**; enlarged in apex of hindwing (Fig. 287G) **[1]**. CI=1; RI=1.

30. If ventral submarginal spots are present (27:0), they are surrounded by white scaling or no additional scaling (e.g. Fig. 287H) **[0]**; bluish-white scaling (e.g. Fig. 287R) **[1]**. CI=1; RI=1.

Male abdomen:

31. Blue scaling over entire dorsal surface of abdomen is absent (e.g. Fig. 286U) **[0]**; present (e.g. Fig. 286R) **[1]**. CI=0.5; RI=91.

32. An isolated patch of smaller, paler coloured scales on dorsum of male abdomen is absent **[0]**; brown and restricted to segment three (Fig. 286M) **[1]**; whitish and present on segments two and three (Fig. 286U) **[2]**. CI=0.5; RI=0.5. See SEM illustration of character states [1] and [2] in Chapter 2 (Fig. 3).

33. A thin, contrasted whitish line along length of ventral abdominal surface is absent (e.g. Fig. 287U) **[0]**; present (Fig. 287J) **[1]**. CI=1; RI=1.

34. Spiracle on abdominal segment three of males is positioned dorsally (Fig. 289A) **[0]**; medially (Fig. 289B) **[1]**; ventrally (Fig. 289C) **[2]**. CI=1; RI=1. NOTE: As the only male abdomen available for *A. drepana* was damaged and no male is known for *A.urichi*, this character was coded from the female abdomen for these two species.

35. Eighth male tergite has a continuously even ventral margin (e.g. Fig. 289H) **[0]**; a sharply indented ventral margin medially (Fig. 289D) **[1]**; a sharply indented ventral margin anteriorly (Fig. 289E) **[2]**. CI=0.5; RI=0.5.

36. A small, ovoid, lightly sclerotised fenestration in middle of eighth male tergite is absent **[0]**; present (Fig. 289I) **[1]**. CI=1; RI=1.

37. Eighth male tergite is symmetrical **[0]**; asymmetrical (Fig. 289J) **[1]**. CI=0.33; RI=0.6.

38. Eighth male tergite is roughly square (length < 6 x width) (e.g. Fig. 289E) **[0]**; elongate (length > 6 x width) (Fig. 289F) **[1]**. CI=0.33; RI=0.5. NOTE: Length is measured from anterior tip to posterior tip; height is measured at a point towards posterior tip.

39. A sclerotised invagination at posterior margin of eighth male tergite is absent **[0]**; present on at least one side of abdomen (e.g. Fig. 289H) **[1]**. CI=0.25; RI=0.89.

40. If a sclerotised invagination is present at posterior margin of eighth male tergite (39:1), it is narrow on both sides of abdomen (Fig. 289H) **[1]**; broad on at least one side of abdomen (Fig. 289J) **[2]**. CI=0.29; RI=0.81.

41. A projection from posterior margin of eighth male tergite is absent **[0]**; typically small, blunt (Fig. 289D) **[1]**; bifurcate (Fig. 289G) **[2]**; typically long, "spike"-like (e.g. Fig. 289H) **[3]**. CI=0.27; RI=0.78. NOTE: Character state [2] is derived from an illustration in Beutelspacher (1981).

42. Anterior margin of eighth male tergite is straight or smoothly rounded (e.g. Fig. 289H) **[0]**; pronouncedly angular (e.g. Fig. 289J) **[1]**. CI=0.17; RI=0.78.

43. A dorsal sclerotised invagination on eighth male sternite is absent **[0]**; present (e.g. Fig. 290B) **[1]**. CI=1; RI=1.

44. If a dorsal sclerotised invagination is present on eighth male sternite (43:1), it is restricted to posterior half of sternite (Fig. 290B) **[1]**; connected to genital armature (e.g. Fig. 291A) **[2]**. CI=1; RI=1.

45. Ventral portion of eighth male sternite is entire (e.g. Fig. 290I) **[0]**; reduced to a tiny vestigial triangle or band (e.g. Fig. 290K) **[1]**. CI=0.5; RI=0.97.

46. Ventral portion of eighth male sternite is symmetrical **[0]**; asymmetrical (Fig. 290B) **[1]**. CI=1; RI=1.

47. Dorsal portion of eighth male sternite is symmetrical **[0]**; asymmetrical (e.g. Fig. 290K) **[1]**. CI=1; RI=1.

48. Lateral projections from eighth male sternite are absent **[0]**; present (e.g. Fig. 290G) **[1]**. CI=0.33; RI=0.93.

49. If lateral projections from eighth male sternite are present (48:1), they are very small (Fig. 290D) **[1]**; small to large (e.g. Fig. 290I) **[2]**. CI=0.5; RI=0.92.

50. Eighth male sternite is a plain rectangle (Fig. 290A) **[0]**; large with two posteriorly pointing projections (Fig. 290B) **[1]**; small, long, narrow and ribbon-like (Fig. 290C) **[2]**; long and of medium width with a small posterior projection and tiny lateral flanges (Fig. 290D) **[3]**; broad with a variably sized posterior projection and small to medium lateral flanges (Fig. 290E) **[4]**; narrowly pointed with small lateral flanges (Fig. 290F) **[5]**; large and laterally compressed, thus narrow in ventral view but broad in lateral view (Fig. 290G) **[6]**; formed into a narrow, posteriorly projecting "horn" (Fig. 290J) **[7]**; broad with a medium to large posterior projection and two very long posterio-dorsal projections (Fig. 290I) **[8]**; formed into two angular posterio-dorsal projections (Fig. 290H) **[9]**; reduced to a vestigial triangle ventrally but dorsal invagination is produced into a very long posterio-dorsal left-hand projection and a shorter right-hand projection (Fig. 290K) **[A]**; reduced to a vestigial triangle ventrally but dorsal invagination is produced into two very long posterio-dorsal projections that are bifurcate towards their tip (Fig. 290L) **[B]**; reduced to a vestigial triangle (Fig. 291D) **[C]**; reduced to a vestigial band (Fig. 291B) **[D]**. CI=0.93; RI=0.98.

Male genitalia:

51. A lightly sclerotised region at posterior margin of uncus is absent **[0]**; present (e.g. Fig. 291B) **[1]**. CI=0.5; RI=0.5.

52. If a lightly sclerotised region at posterior margin of uncus is present (51:1), it does not extend to leave a heavily sclerotised triangle at lower corner (e.g. Fig. 291B) **[1]**; does extend to leave a heavily sclerotised triangle at lower corner (Fig. 291D) **[2]**. CI=0.67; RI=0.75.

53. A small anterior region devoid of setae on dorsal portion of uncus is absent **[0]**; present (Fig. 291C) **[1]**. CI=0.25; RI=0.75.

54. Setae on uncus are evenly distributed **[0]**; largely restricted to dorsal half (e.g. Fig. 291A) **[1]**. CI=0.25; RI=0.4.

55. A large, upper posterior extension to uncus that is differentiated from lower portion is absent (e.g. Fig. 292D) **[0]**; present (e.g. Fig. 292G) **[1]**. CI=1; RI=1.

56. Upper portion of uncus is rounded (e.g. Fig. 292F) **[0]**; downwardly pointed (e.g. Fig. 292G) **[1]**. CI=1; RI=1.

57. Lower portion of uncus is undifferentiated from upper portion or evenly triangular (e.g. Fig. 292B) **[0]**; triangular and downwardly pointed (Fig. 292E) **[1]**; a narrowly elongate triangle (Fig. 292F) **[2]**; a broadly elongate triangle (Fig. 292A) **[3]**; produced into one or two small points (e.g. Fig. 292C) **[4]**. CI=0.8; RI=0.96.

58. Tegumen is an approximate triangle (e.g. Fig. 292C) **[0]**; a narrow rectangle (Fig. 292B) **[1]**; very elongate, especially in lower anterior corner (Fig. 292E) **[2]**. CI=0.67; RI=0.75.

59. Falci are of average length and width (e.g. Fig. 292C) **[0]**; very long and thin (Fig. 292H) **[1]**; compact and squarely angular (Fig. 292D) **[2]**; bulbously rounded (Fig. 292B) **[3]**; rectangular at base (> 90°), lower edge convex, remainder long and upwardly pointed (e.g. Fig. 292F) **[4]**; dorso-ventrally compressed (Fig. 292I) **[5]**; rectangular at base (< 90°), lower edge straight or concave, remainder short, straight and pointed (e.g. Fig. 292G) **[6]**; rectangular at base (< 90°), lower edge convex, remainder long and rounded, often with tip turned outwards (Fig. 292E) **[7]**. CI=1; RI=1.

60. Vinculum extends from anterior edge of tegumen to beyond top of valvae (e.g. Fig. 291B) **[0]**; top of valvae (Fig. 291D) **[1]**. CI=1; RI=1.

61. A posterior projection from medial region of vinculum is absent **[0]**; present (e.g. Fig. 292K) **[1]**. CI=1; RI=1.

62. If a posterior projection from medial region of vinculum is present (61:1), it is a small "hump" (Fig. 292K) **[1]**; an elongate triangle (Fig. 292L) **[2]**. CI=1; RI=1.

63. A posterior projection from upper region of vinculum is absent **[0]**; present (e.g. Fig. 292M) **[1]**. CI=1; RI=1.

64. If a posterior projection from upper region of vinculum is present (63:1), it is long and triangular on both sides (Fig. 292M) **[1]**; very long and "paddle"-shaped on at least one side (Fig. 292N) **[2]**. CI=0.67; RI=0.8.

65. Vinculum is symmetrical **[0]**; asymmetrical (Fig. 292N) **[1]**. CI=0.5; RI=0.67.

66. Vinculum forms a true anterior saccus (Fig. 292J) **[0]**; a ventral, anterior "bulb" (Fig. 291A) **[1]**; a ventral, posterior "cup" (Fig. 291B) **[2]**; no anterior or posterior shapes ventrally (e.g. Fig. 292N) **[3]**. CI=0.75; RI=0.9.

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67. Valvae are narrow, elongate and pointed (Fig. 293A) **[0]**; very large and broad with two rounded projections (Fig. 293D) **[1]**; large and broad with single, "bird's-head"-shaped upper projection (Fig. 293C) **[2]**; broad with narrow, upwardly pointed upper projection and rounded lower projection (Fig. 293B) **[3]**; small with upwardly pointed upper projection and smaller lower projection (Fig. 293G) **[4]**; narrow with prominent basal lateral bulge and narrow upwardly pointed projection (Fig. 293H) **[5]**; small and narrow with one or two rounded points at tip (Fig. 293F) **[6]**; large, posteriorly elongate and rounded at tip (Fig. 293I) [7]; square or rectangular with concave distal margin (Fig. 293J) **[8]**; roundly rectangular with single posteriorly projecting point at middle of distal margin (Fig. 293K) [9]; dorsally elongate and narrow with short basal lateral bulge (Fig. 293N) **[A]**; large and dorsally very elongate with posteriorly projecting semicircle at dorsal tip (e.g. Fig. 293M) **[B]**; variably elongate with distal undulations and concave anterior margin towards tip (Fig. 293L) [C]; large and markedly bifurcate with very long and narrow lower projection and large basal lateral bulge (Fig. 293E) **[D]**; dorsally elongate and narrow, twisted towards rounded tip (e.g. Fig. 293S) **[E]**; large and bifurcate with prominent basal lateral bulge and narrow posterior projection at middle of distal margin that broadens at tip (Fig. 293R) **[F]**; large, narrow and dorsally elongate with equally broad anterior margin (Fig. 293O) **[G]**; large with variably elongate, narrow upper posterior projection (an upper "arm") (e.g. Fig. 293U) **[H]**; triangular and dorsally elongate, tilted inwards dorsally over aedeagus with tips splayed outwards (Fig. 293Q) **[I]**; narrow with basal lateral bulge of same length as remainder (Fig. 293P) **[J]**. CI=0.1; RI=0.1.

68. If upper "arms" to valvae are present (67:H) they are small (Fig. 293T) **[1]**; long (Fig. 293U) **[2]**; very long (Fig. 293V) **[3]**. CI=1; RI=1.

69. If upper "arms" to valvae are present (67:H), a basal "hump" is absent **[1]**; present (Fig. 293V) **[2]**. CI=1; RI=1.

70. If upper "arms" to valvae are present (67:H), in dorsal view these lie close together at base (e.g. Fig. 293U) **[1]**; are distantly separated at base (Fig. 293V) **[2]**. CI=1; RI=1.

71. Posterior portion of aedeagus is straight or downturned (e.g. Fig. 294E) **[0]**; upturned (e.g. Fig. 294H) **[1]**. CI=0.33; RI=0.93.

72. Tip of aedeagus is variably pointed or rounded (e.g. Fig. 294B) **[0]**; abruptly upturned and vertically broad (Fig. 294G) **[1]**; bulbous and "basket"-shaped (e.g. Fig. 294I) **[2]**. CI=1; RI=1.

73. If tip of aedeagus is bulbous and "basket"-shaped (72:2) it is small, well sclerotised and highly torsional (Fig. 294I) **[1]**; large and semi-sclerotised (Fig. 291D) **[2]**. CI=1; RI=1.

74. Lightly sclerotised lateral tissue towards tip of aedeagus is absent **[0]**; present (Fig. 294D) **[1]**. CI=1; RI=1.

75. Aedeagal tip opens upwards, posteriorly or weakly to the left (e.g. Fig. 294F) **[0]**; markedly to the right (Fig. 294C) **[1]**. CI=0.5; RI=0.67.

76. Aedeagus is straight towards anterior end (e.g. Fig. 294E) **[0]**; contorted towards anterior end (e.g. Fig. 294I) **[1]**. CI=0.33; RI=0.9.

77. Soft tissue at anterior tip of aedeagus is directed anteriorly (e.g. Fig. 294G) **[0]**; ventrally (Fig. 294C) **[1]**. CI=1; RI=1.

78. A sclerotised plate inside aedeagus is absent **[0]**; present (Fig. 294G) **[1]**. CI=1; RI=1. NOTE: This character is coded separately from the following as it varies independently.

79. Aedeagus contains several sparsely distributed, variably elongate and heavily sclerotised pencillate cornuti (Fig. 294B) **[0]**; a long band of numerous small, triangular and oval cornuti (Fig. 294C) **[1]**; numerous, densely packed long pencillate cornuti (Fig. 291A) **[2]**; a single large crescent-shaped cornutus (Fig. 294A) **[3]**; a single, elongate and narrow cornutus that parallels distal edge of aedeagus when everted (Fig. 294D) **[4]**; one or more triangular cornuti that are heavily sclerotised only at tip and project anteriorly when everted (e.g. Fig. 294E) **[5]**; a single, large, arrow-shaped cornutus (Fig. 294G) **[6]**; one or typically more, medium sized, triangular or tear-drop shaped cornuti (Fig. 291D) **[7]**; no internal cornuti or only tiny sclerotised structures (e.g. Fig. 294H) **[8]**. CI=1; RI=1.

80. If one or more triangular cornuti that are heavily sclerotised only at tip are present (79:5), these are solitary (Fig. 294E) **[1]**; paired (Fig. 294F) **[2]**. CI=1; RI=1.

81. Pedicel is normal and strap-like (Fig. 291B) **[0]**; is laterally thickened (Fig. 291A) **[1]**; consists of a well sclerotised base with lightly sclerotised remainder (Fig. 291D) **[2]**. CI=0.5; RI=0.85.

82. Pedicel is symmetrical **[0]**; asymmetrical (e.g. Fig. 294J) **[1]**. CI=1; RI=1.

83. If pedicel is asymmetrical (82:1), this asymmetry is weak (Fig. 294J) **[1]**; very pronounced (Fig. 294K) **[2]**. CI=1; RI=1.

Female abdomen and genitalia:

84. A heavily sclerotised disc at upper posterior margin of last tergite is absent **[0]**; present (e.g. Fig. 296B) **[1]**. CI=0.25; RI=0.84.

85. If a heavily sclerotised disc at upper posterior margin of last tergite is present (84:1), it is small and semicircular (Fig. 296A) **[1]**; posteriorly elongate (Fig. 296B) **[2]**. CI=0.33; RI=0.8.

86. A variably sclerotised plate with a pair of indentations between ostium bursae and papillae anales is absent **[0]**; present (Fig. 296F) **[1]**. CI=0.5; RI=0.67.

87. Ostium bursae consists of a sclerotised ring (e.g. Fig. 295B) **[0]**; has no entire sclerotised dorsal portion but only a tiny sclerotised triangle at each dorsal corner (Fig. 296G) **[1]**; has no sclerotised dorsal portion (e.g. Fig. 296E) **[2]**; has no sclerotised ventral portion (Fig. 296H) **[3]**. CI=0.38; RI=0.67.

88. If ostium bursae consists of a sclerotised ring (87:0), it is variably round (e.g. Fig. 295B) **[0]**; elongate and shaped like an "open mouth" (Fig. 295A) **[1]**. CI=1; RI=1.

89. If ostium bursae consists of a sclerotised ring (87:0), an elongate dorso-lateral projection on either side is absent **[0]**; present (Fig. 295D) **[1]**. CI=1; RI=1.

90. Ventral portion of ostium bursae is straight or evenly rounded (Fig. 296I) **[0]**; formed into an angular "U"-shape with the tips as broad as or broader than the base (Fig. 296E) **[1]**. CI=1; RI=1. NOTE: The single taxon, *senta*, which has no ventral portion to ostium bursae is coded with character state (?).

91. A triangular, posteriorly concave, anterio-lateral projection on either side of ostium bursae is absent **[0]**; present (Fig. 296J) **[1]**. CI=1; RI=1.

92. Significant amounts of heavy sclerotisation in posterior half of ductus bursae are absent (e.g. Fig. 295B) **[0]**; present and shorter in length than corpus bursae (e.g. Fig. 295D) **[1]**; present and equal in length to corpus bursae (Fig. 295A) **[2]**. CI=0.29; RI=0.64.

93. Posterior half of ductus bursae is straight (e.g. Fig. 295A) **[0]**; to some degree coiled (Fig. 295C) **[1]**. CI=0.5; RI=0.67.

94. Posterior half of ductus bursae is approximately parallel with abdomen (e.g. Fig. 295B) **[0]**; angled dorsally towards papillae anales, creating right angle with remainder of ductus bursae (Fig. 295D) **[1]**. CI=1; RI=1.

95. A hollow, medially divided, sclerotised ovoid structure in ductus bursae opposite opening to ductus seminalis is absent **[0]**; present (e.g. Fig. 296C) **[1]**. CI=1; RI=1.

96. If a hollow, medially divided, sclerotised ovoid structure in ductus bursae opposite opening to ductus seminalis is present (95:1), it is short (Fig. 296D) **[1]**; long (Fig. 296C) **[2]**. CI=1; RI=1.

97. If a hollow, medially divided, sclerotised ovoid structure in ductus bursae opposite opening to ductus seminalis is present (95:1), it is positioned close to ostium bursae (Fig. 296C) **[1]**; far from ostium bursae (Fig. 296D) **[2]**. CI=1; RI=1.

98. A small, heavily sclerotised "bean"-shaped structure in ductus bursae between ductus seminalis and opening to corpus bursae is absent **[0]**; present (Fig. 295A) **[1]**. CI=1; RI=1.

99. Ductus seminalis is a small tube extending at approximate right angle from ductus bursae (e.g. Fig. 295A) **[0]**; a broad tube extending in seemless straight line from middle of ductus bursae; posterior portion of ductus bursae extends from this junction as smaller tube (Fig. 295D) **[1]**. CI=1; RI=1.

100. Ductus seminalis is not hardened **[0]**; hardened (but not sclerotised) with studded sculpturing (Fig. 295B) **[1]**. CI=0.5; RI=0.83.

101. Signae form sclerotised bands (Fig. 295E) **[0]**; form sclerotised invaginations (e.g. Fig. 295C) **[1]**; are absent **[2]**. CI=0.67; RI=0.8.

102. If signae form sclerotised invaginations (101:1), their openings at wall of corpus bursae are broadest horizontally (Fig. 297A) **[1]**; vertically (e.g. Fig. 297G) **[2]**. CI=0.5; RI=0.33.

103. If signae form sclerotised invaginations with vertical openings (102:2), these are a small, approximate semicircle or rectangle (Fig. 297D) **[1]**; a small triangle (e.g. Fig. 297E) **[2]**; rounded with a concave distal margin (Fig. 297J) **[3]**; symmetrically pointed at posterior and anterior tips (Fig. 297C) **[4]**; small and narrowly pointed (Fig. 297B) **[5]**; rectangular with small pointed tip (Fig. 297K) **[6]**; elongate at base with serrate inner edge and roundly pointed tip (e.g. Fig. 297L) **[7]**; very large and elongate at base with serrate inner edge and broadly pointed tip (Fig. 297G) **[8]**; a sharply pointed triangle with concave anterior margin (e.g. Fig. 297I) **[9]**; very large and elongate at base with very long roundly pointed tip (Fig. 297F) **[A]**; very large and elongate at base with very large and broadly rounded tip (e.g. Fig. 297H) **[B]**. CI=0.85; RI=0.93.

104. If invaginated signae are very large and elongate at base with very large and broadly rounded tip (103:B), transverse creases across their surface are absent (Fig. 295A) **[1]**; present (Fig. 297H) **[2]**. CI=1; RI=1.

Fig. 288. The strict consensus tree for the subtribe Theopeiti based on the characters in Table 9, after four iterations of successive weighting. Clades of generic worth are marked with the encircled letters A-E and those of species group worth within *Theope* are marked with the encircled numbers 1-13; universal synapomorphies for these clades are listed in Tables 10 and 11 respectively. Branch support, in the form of bootstrap values above 50, is given above relevant branches.

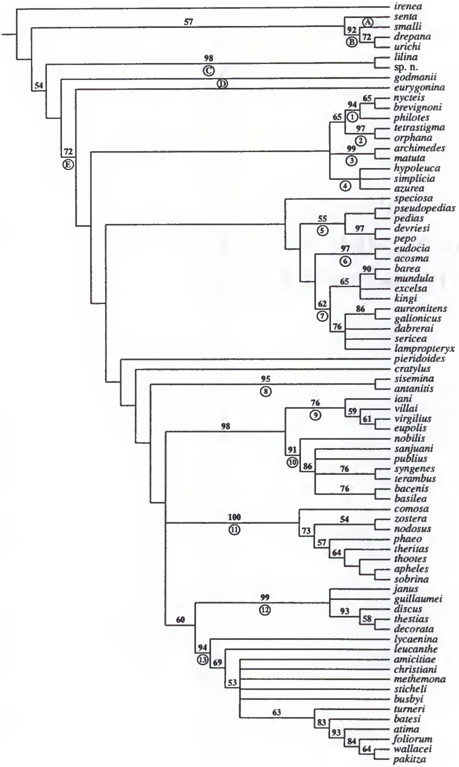

irenea
57
Ⓐ
senta
smalli
92
72
Ⓑ
drepana
urichi
98
lilina
Ⓒ
sp. n.
54
godmanii
Ⓓ
eurygonina
65
nycteis
94
brevignoni
65
①
philotes
97
tetrastigma
②
orphana
72
99
archimedes
Ⓔ
③
matuta
hypoleuca
simplicia
④
azurea
speciosa
pseudopedias
55
pedias
⑤
97
devriesi
pepo
97
eudocia
⑥
acosma
90
barea
mundula
65
excelsa
kingi
62
86
aureonitens
⑦
galionicus
76
dabrerai
sericea
lampropteryx
pieridoides
cratylus
95
sisemina
⑧
antanitis
iani
76
villai
⑨
59
61
virgilius
98
eupolis
nobilis
91
sanjuani
⑩
86
publius
76
syngenes
terambus
76
bacenis
basilea
comosa
100
54
zostera
⑪
73
nodosus
57
phaeo
64
theritas
thootes
apheles
sobrina
janus
99
guillaumei
⑫
93
discus
58
thestias
60
decorata
lycaenina
94
leucanthe
⑬
69
amicitiae
christiani
53
methemona
sticheli
busbyi
63
turneri
83
batesi
93
atima
84
foliorum
64
wallacei
pakitza

Table 10. Universal synapomorphies (or autapomorphies) for the clades of generic worth in the Theopeiti. The letters A-E preceding the taxa refer to nodes in Figure 288, the numbers in parentheses after each taxon represent the number of species it contains, the numbers in parentheses after apomorphies refer to the character number and state in this study (see Table 9), and the symbols [-] and [+] refer to apomorphies unique to the Theopeiti only and the entire Nymphidiini (*sensu* Harvey, 1987) respectively. Reference is given to figure numbers where appropriate.

Taxon	Synapomorphies/autapomorphies
A *senta* [1]	• Dorsal surface a mottled orange pattern [5:1] [-] (Fig. 286B) • Spiracle on abdominal segment 3 of males positioned medially [34:1] [-] (Fig. 289B) • Uncus of male genitalia very long [+] • Posterior margin of uncus of male genitalia sharply notched in dorsal view [-] • Falci of male genitalia very long and narrow [59:1] [+] (Fig. 292H) • Valvae of male genitalia narrow, elongate and downwardly pointed [67:0] [-] (Fig. 293A) • Signae of female genitalia consist of sclerotised bands on surface of corpus bursae instead of invaginations [101:0] [-] (Fig. 295E)
B *Archaeonympha* [3]	• Ductus bursae of female genitalia possesses an elongate, hollow, posteriorly medially divided, sclerotised structure opposite opening of ductus seminalis (Hall & Harvey, 1998) [95:1] [+] (Fig. 296C)
C *lilina* group [2]	• A white triangle at middle of dorsal forewing costa present [6:1] [-] (Fig. 286E) • Posterior portion of last male sternite heavily sclerotised and produced into two long, asymmetrical points [46:1] [+] (Fig. 290B) • Valvae of male genitalia broad with single broad, "bird's-head"-shaped upper projection [67:2] [+] (Fig. 293C) • Soft tissue at anterior tip of aedeagus of male genitalia directed ventrally instead of anteriorly [77:1] [-] (Fig. 294C) • Aedeagus of male genitalia contains long band of oval-shaped cornuti [79:1] [+] (Fig. 294C)
D *godmanii* [1]	• Forewing apices produced into long points [-] (Fig. 286F) • Narrow, white, curving postdiscal band on forewing present [-] (Fig. 286F) • Posterior portion of last male sternite heavily sclerotised and produced into two short, symmetrical points [-] • Valvae of male genitalia broad with concave distal margin [67:1] [+] (Fig. 293D) • Aedeagus of male genitalia contains single large crescent-shaped cornutus [79:3] [+] (Fig. 294A)
E *Theope* [68]	• Two spots at base of cell 1A+2A on ventral forewing absent [20:1] [-] (see Fig. 287) • A continuous, well sclerotised dorsal invagination joins eighth male sternite to genital armature [44:2] [+] (Fig. 291A)

Table 11. Universal synapomorphies for the clades worthy of species group recognition in *Theope* (adapted from Hall, 1999). The numbers 1-13 preceding each species group name refer to nodes in Figure 288, the numbers in parentheses after each species group name represent the number of species it contains, and the numbers in parentheses after each synapomorphy refer to the character number and state in this study (see Table 9). Reference is given to figure numbers where appropriate.

Theope group	Synapomorphies
1 *nycteis* [3]	• Submarginal spots on ventral hindwing enlarged in apex [29:1] (Fig. 287G) • Last male sternite long, thin and ribbon-like with no lateral projections [50:2] (Fig. 290C)
2 *tetrastigma* [2]	• Aedeagus of male genitalia possesses lightly sclerotised tissue laterally towards tip [74:1] (Fig. 294D) • Aedeagus of male genitalia contains single, elongate and narrow cornutus that parallels distal edge of aedeagus when everted [79:4] (Fig. 294D)
3 *hypoleuca* [3]	• None
4 *archimedes* [2]	• Red scaling present at base of ventral forewing [18:1] (Fig. 287J) • Thin, contrasted whitish line present along length of ventral abdominal surface [33:1] (Fig. 287J) • Lower portion of uncus of male genitalia a broadly elongate triangle [57:3] (Fig. 292A) • Valvae of male genitalia evenly posteriorly elongate and rounded at tip [67:7] (Fig. 293I) • Dorsal portion of ostium bursae of female genitalia reduced to a sclerotised triangle in each corner [87:1] (Fig. 296G)
5 *pedias* [4]	• None
6 *eudocia* [2]	• Dorsal surface predominantly a uniform orange [5:2] (Fig. 286M) • Valvae of male genitalia rectangular with single posteriorly projecting point from middle of distal margin [67:9] (Fig. 293K)
7 *sericea* [9]	• Signae of female genitalia large and "horn"-shaped [103:A] (Fig. 297F)
8 *antanitis* [2]	• Medial white band present on both ventral surfaces [23:1] (Fig. 287O) • Valvae of male genitalia narrow with basal lateral bulge of same length as remainder [67:J] (Fig. 293P)
9 *virgilius* [4]	• Last male sternite "horn"-shaped [50:7] (Fig. 290J) • Medial region of vinculum of male genitalia possesses a "hump"-like posterior projection [62:1] (Fig. 292K)
10 *terambus* [7]	• Medial region of vinculum of male genitalia possesses an elongate, triangular posterior projection [62:2] (Fig. 292L) • Aedeagus contains single large, arrow-shaped cornutus [78:6] (Fig. 294G) • Ostium bursae of female genitalia laterally elongate and shaped like an "open mouth" [88:1] (Fig. 295A) • Signae of female genitalia very large and elongate with a broadly rounded tip [102:B] (Figs. 295A, 297H)
11 *theritas* [8]	• Base of forewing costa strongly bowed [2:1] (Fig. 286T) • Elongate postdiscal blue on dorsal forewing of females present in cells M_2 and M_1 only [10:1] (Fig. 286U) • Last male sternite asymmetrical [47:1] (Fig. 290K) • Dorsal portion of last male sternite consists of two posterio-dorsal projections, a very long left-hand "arm" and a typically shorter right-hand "arm" [50:A] (Fig. 290K) • Lower portion of uncus of male genitalia triangular and downwardly pointed [57:1] (Fig. 292E) • Falci of male genitalia angularly rectangular at base (<90°), lower edge convex, remainder long and rounded, typically with tip turned outwards [59:7] (Fig. 292E) • Upper region of vinculum of male genitalia possesses an elongate posterior projection [63:1] (Figs. 292M,N) • Pedicel of male genitalia asymmetrical [82:1] (Fig. 294J)
12 *thestias* [5]	• Prominent yellow scaling present at base only of ventral forewing [16:1] (Fig. 287V) • Last male sternite reduced to a vestigial band [50:D] (Fig. 291B) • Lower portion of uncus of male genitalia a narrowly elongate triangle [57:2] (Fig. 292F) • Vinculum of male genitalia forms a ventral, posterior "cup" [66:2] (Fig. 291B) • Valvae of male genitalia narrow and twisted [67:E] (Fig. 293S) • Ostium bursae of female genitalia possesses two posteriorly concave and triangular anterio-lateral projections [91:1] (Fig. 296J)
13 *foliorum* [13]	• Vinculum of male genitalia incomplete, extending from anterior edge of tegumen to top of valvae [60:1] (Fig. 291D) • Valvae of male genitalia possess an upper posterior projection or "arm" [67:H] (Figs. 293T,U,V)

rounds of successive weighting at 1000 MPTs to maintain computing time within practical limits. Successive weighting resulted in the stabilisation of character weights after four iterations and the strict consensus tree of the final 1000 MPTs is presented (Fig. 288) as the best current hypothesis of relationships within the Theopeiti and will represent the focus of subsequent discussion. This consensus tree has a length of 176.7, a consistency index (CI) of 0.76, and a retention index (RI) of 0.89. Note that the tree length is not represented by an integer since fractional weights have been used.

There are several points of interest concerning this cladistic result. The high consistency index, which is actually extraordinarily high given the large number of taxa in the data set (see Sanderson & Donoghue, 1989), is indicative of a low level of homoplasy, a result that in this case has also led to very high bootstrap support for a great many clades. Two of the three polytypic clades deemed on morphological and ecological grounds to be of generic worth have bootstrap values above 90, as do 9 of the 13 clades similarly deemed to be of species group worth within the largest genus *Theope*; universal synapomorphies for all the recognised generic clades (A-E in Fig. 288) and species group clades (1-13 in Fig. 288) are listed in Tables 10 and 11 respectively. The only numbered clade in Figure 288 for which no bootstrap value above 50 is given is the "*hypoleuca* group" of *Theope* (clade 4), and its monophyly is uncertain. It is generally noticeable that branch support (i.e. confidence in topological resolution) is somewhat lower for the more plesiomorphic clades within *Theope* than the most derived ones.

Character Evolution

Since details of the cladistic analysis can be retrieved from the character list (Table 9) and matrix (Appendix C), and universal synapomorphies for the major clades of interest are listed in Tables 10 and 11, what follows is a broad overview of character evolution in the Theopeiti. All clade numbers refer to those in Figure 288.

It is first important to mention those morphological traits not associated with the character sets discussed below that were examined but not coded, and why. Antennal structure is relatively homogeneous across the Papilionoidea, and a SEM figure of a representative *Theope* antennal segment is given in Chapter 2. As is typical for myrmecophilous species, the extent of the nudum is great, especially in females (Forbes, 1957; Robbins, 1991), but this character exhibits continuous interspecific variation, as does club shape and the number of shaft segments, which I found to be directly correlated with the size of the butterfly. The eyes of all species in the Theopeiti are bare, and, not unexpectedly at this taxonomic level (Eliot, 1973), no qualitative variation could be found in the structure of the eyes and proboscis of two phylogenetically disparate species examined under the SEM. The second and particularly the third palpal segments exhibit substantial interspecific and sexual variation in length, independent of overall size of the butterfly, the third segment varying from very short in, for example, "*Pandemos*" *godmanii*, to very long in, for example, "*pedias* group" species of *Theope*; however, across this very large data set no suitably large gaps could be observed in this variation to permit theoretically sound coding. The range of palpal variation for *Theope* is illustrated in Chapter 2. Forelegs and midlegs were examined for eight phylogenetically disparate species in the Theopeiti, but no qualitative variation could be found; the typical leg structure of *Theope* is figured in Chapter 2, that of *Archaeonympha* in Chapter 3. Despite significant interspecific variation, the colors of ventral appendages could not be coded because they did not vary independently from ventral wing coloration.

The use of wing venational characters in the classification of the Lepidoptera has a long history (Herrich-Schäffer, 1843-1856; Comstock & Needham, 1918; Heppner, 1998), but at low taxonomic levels in the Riodinidae, I have found such characters to be so homoplesious as to be essentially useless for inferring phylogeny. Forewing radial venation in the Theopeiti is highly variable between species and the extent of fusion between veins R1 and Sc varies from none to complete fusion along their entire length, superficially reducing the number of radial veins to four. The high degree of homoplasy in this character is well demonstrated by the independent evolution of the most extreme case of fusion in two phylogenetically disparate groups of *Theope*, the "*tetrastigma*" (clade 2) and "*thestias* groups" (clade 12); in the former case, Stichel (1911) actually cited the fusion of veins R1 and Sc as the predominant reason for describing his now synonymised genus *Dinoplotis*. Irrespective of the homoplasy inherent in this character, it was too continuously variable to be able to code.

Behavioral ecology

The use of behavioral ecological characters in phylogenetic reconstruction is controversial (see Miller & Wenzel, 1995, and references therein) since their states are often difficult to define and homologise and deemed to be too evolutionarily labile even at low taxonomic levels. However, there is increasing support for the use of such characters, and in a broad comparison of behavioral and morphological data sets, DeQueiroz & Wimberger (1991) found that the overall CI's of each, and thus levels of homology, did not significantly differ. I was able to include one behavioral character that did not seem to suffer from the aforementioned problems, namely resting posture. The Riodinidae is unusual amongst the Papilionoidea in that the majority of its members rest with their wings outspread (e.g. see Krizek, 1991); however, a few genera have reverted to the plesiomorphic condition of resting with the wings closed and folded over the body (DeVries, 1997; pers. obs.). In the tribe Nymphidiini, this resting posture occurs once in the Nymphidiiti, in the genus *Setabis* Westwood, and appears to reoccur only once in the Theopeiti, grouping "*Pandemos*" *godmanii* with *Theope*; however, the apomorphic state for *godmanii* is based on a single observation of a female in DeVries (1997) and needs confirmation. The apomorphic state for resting posture is expected to occur in all *Theope* species.

Wing shape and pattern

Again, wing pattern characters are also often purposely omitted from cladistic analyses due to concerns about homology. In general, it is certainly true that the evolutionary processes of sexual and natural selection, particularly when resulting in selection for mimicry (Vane-Wright & Smith, 1991; Brower, 1994; Miller, 1996), can lead to extensive wing pattern convergence, but at relatively low taxonomic levels in which mimicry is not a factor, such as is the case in this study, wing pattern characters can provide very valuable phylogenetic information. Indeed, although the three main character sets of wing pattern, male and female genitalia, all have similar CI's, the wing pattern character set actually has the highest CI (0.79).

Overall, wing pattern characters tend to provide corroborating evidence for the monophyly of clades delineated by genitalic characters, but they only provide universal synapomorphies for 6 of the 13 species groups within *Theope*. The most obvious trend in wing pattern evolution in the Theopeiti is the gradual reduction in ventral wing markings (see Fig. 287), and the complete lack of any ventral markings on many species of the most derived genus, *Theope*, is superficially one of the most characteristic features of that genus. This evolutionary pattern has provided one of only two universal synapomorphies for *Theope* (Table 10), the total absence of any spots or rare presence of a single spot (e.g. *T. eurygonina*) instead of two at the base of cell Cu2 on the ventral forewing (Fig.

287). This loss also occurs several times in the Nymphidiiti, in the genera *Setabis*, *Pandemos* Hübner, and *Zelotaea* Bates (Hall, in prep.), but a uniformly colored, patternless ventral surface is unique within the Riodinidae to *Theope*, as are the gaudy orange ("*pedias* group" - clade 5) and yellow ("*eudocia*" and "*sericea* groups" - clades 6 and 7) ventral colors of many species (see Figs. 287K-N).

Possibly one of the most unusual ventral wing patterns in the Theopeiti occurs in species of the plesiomorphic "*nycteis* group" of *Theope* (clade 1), which exhibit fine-grained, undulating yellow banding, termed a "ripple pattern" by Nijhout (1991) (see Fig. 287G). This pattern is found nowhere else in the Riodinidae, although it is common in the nymphalid subfamilies Satyrinae and Brassolinae, and it is the main reason why "*nycteis* group" species were treated in the separate genus *Parnes* Westwood, until this work. It is only through cladistic analyses that this wing pattern has been hypothesised to have evolved from a typical *Theope*-like ancestor, probably a species similar to *T. tetrastigma* (clade 2) (Figs. 286H,287H). It is probable that, as in species of the aforementioned nymphalid groups, this wing pattern divergence has resulted from an adaptation to living in the gloomy forest understorey, an ecological trait restricted within the Theopeiti to the "*nycteis*" and, to a slightly lesser extent, "*tetrastigma* groups" of *Theope*.

Another set of external morphological traits documented to occur in the Theopeiti, but only rarely elsewhere in the Nymphidiini, is male androconia. The physiological function of many scale types is still uncertain (Downey & Allyn, 1975; Scoble, 1991), but many *Theope* species possess what appear to be androconial scales in the postdiscal area of the dorsal forewing (Figs. 287N,R,S), and yet others possess more highly modified androconial scales on certain dorsal segments of the abdomen (Figs. 287M,T) (see Chapter 2 for SEM illustrations). Since the wing androconia occur in three disparate species groups, the "*sericea*", "*terambus*" and "*foliorum* groups" (clades 7, 10 and 13), and the external abdominal androconia occur in a further two disparate groups (3 species groups), the "*pedias* + *eudocia*" and "*theritas* groups" (clades 5, 6 and 11), it is clear that such characters are highly plastic and repeatedly selected for. It is unclear why some species or species groups possess androconia and others do not.

Male genitalia and abdomen

As outlined in the introduction, Harvey (1987) used the ventral (Fig. 289C) instead of dorsal (Fig. 289A) position of the spiracle on male abdominal segment three to define his tribe Nymphidiini, a character state that is found in both adults and larvae (Harvey, 1987). Although there are several plesiomorphic genera in the subtribe Nymphidiiti that actually possess a medially positioned spiracle (Fig. 289B) (Hall, in prep.), the only taxon to possess this character state in the Theopeiti is its apparently most plesiomorphic taxon, "*Adelotypa*" *senta*. The shape of the spiracle is interspecifically highly variable, as is the spiracle's exact position, which was measured with respect to the two sclerites for each species, but discrete bands of variation could not be delineated for either character.

The elaborate modifications of the terminal (eighth) sclerites (Figs. 289 and 290) in members of the Theopeiti are unparalleled in the Riodinidae, and are especially varied and ubiquitous in the genus *Theope*. Such structures occur sporadically throughout the Lepidoptera, and their function appears to be to aid in clasping the female abdomen during copulation, in conjunction with the genitalic valvae (Miller, 1988, 1996). Their exact form provides excellent clues as to species group membership in *Theope*, as evidenced by the CI of 0.93 for the 13 state character 50 describing sternite shape. Posterior projections from the last tergite are found nowhere else in the family but in *Theope* (Figs. 289G,H,J), although not all species possess them. Such projections occur

Fig. 289. Representative male abdominal sclerites for the Theopeiti, illustrating characters 34-42 in Table 9. Figs. A-C represent the spiracle position on abominal segment three for the following species: **A**: *Thisbe irenea*; **B**: *"Adelotypa" senta*; **C**: *Theope lampropteryx*. Figs D-J represent the last (eighth) tergite in lateral view (on both sides of the abdomen for Fig. J) for the following species: **D**: *Archaeonympha drepana*; **E**: *Theope tetrastigma*; **F**: *Theope sericea*; **G**: *Theope villai* (adapted from Beutelspacher (1981)); **H**: *Theope basilea*; **I**: *Theope methemona*; **J**: *Theope theritas*.

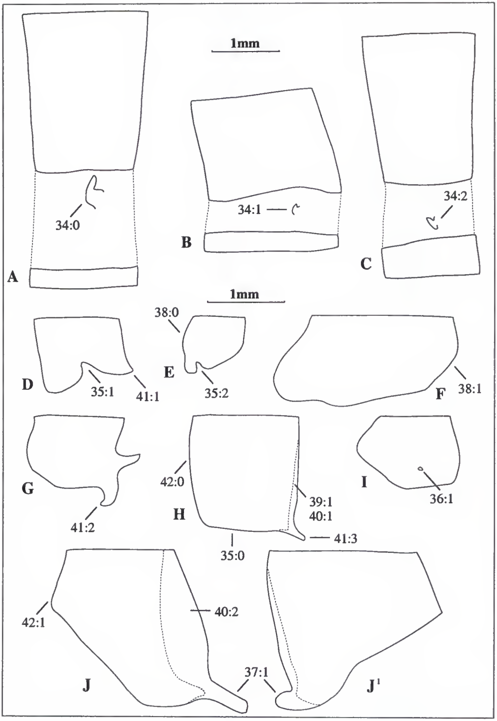

1mm
34:0
A
34:1
B
34:2
C
1mm
38:0
D
35:1
41:1
E
35:2
F
38:1
G
41:2
42:0
H
39:1
40:1
41:3
35:0
I
36:1
42:1
40:2
J
37:1
J¹

Fig. 290. Representative last (eighth) male abdominal sternites for the Theopeiti, illustrating characters 43-50 in Table 9. All sternites are figured in ventral view, but those in Figs. C-L are also figured in lateral view (marked with a superscript 1). **A**: *Archaeonympha drepana*; **B**: "*Calociasma*" *lilina*; **C**: *Theope nycteis*; **D**: *Theope archimedes archimedes*; **E**: *Theope pepo*; **F**: *Theope eudocia*; **G**: *Theope galionicus*; **H**: *Theope pieridoides*; **I**: *Theope antanitis*; **J**: *Theope virgilius*; **K**: *Theope nodosus*; **L**: *Theope sobrina.*

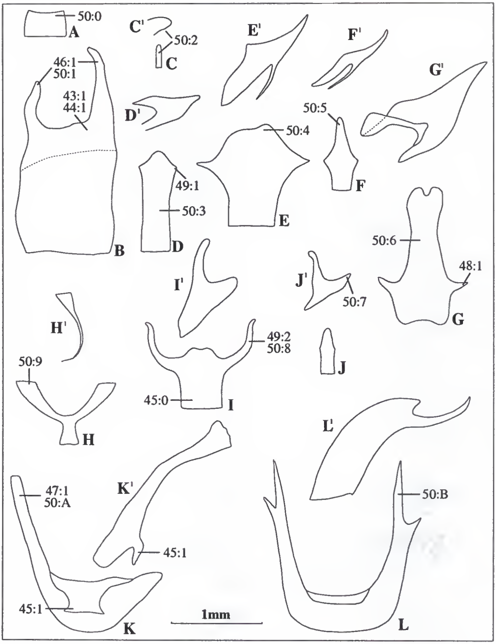

50:0
A
C'
50:2
C
E'
F'
G'
46:1
50:1
43:1
44:1
D'
50:5
50:4
49:1
50:3
E
F
B
D
50:6
48:1
I'
J'
50:7
G
H'
49:2
50:8
50:9
J
45:0
I
H
L'
47:1
50:A
K'
50:B
45:1
45:1
1mm
K
L

Fig. 291. Selected male genitalia of the Theopeiti, illustrating characters 44, 50-54, 60, 66, 73, 79, and 81 in Table 9. Fig. C represents an uncus in dorsal view, the remainder represent the entire genital armature, with eighth sternite attached, in lateral view. **A**: *Theope sericea*; **B** : *Theope thestias*; **C**: *Theope virgilius*; **D**: *Theope wallacei.* Abbreviations on Fig. A: **Te** - Tegumen; **Un** - Uncus; **Fa** - Falcus; **Vi** - Vinculum; **Va** - Valva; **Ae** - Aedeagus; **Co** - Cornutus; **Pe** - Pedicel; **St** - Eighth sternite.

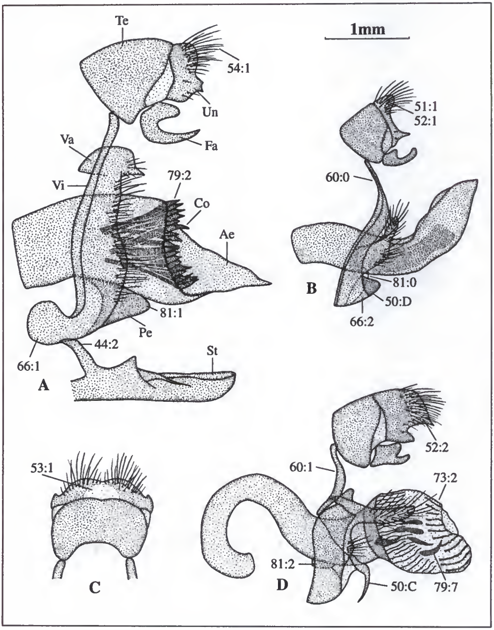
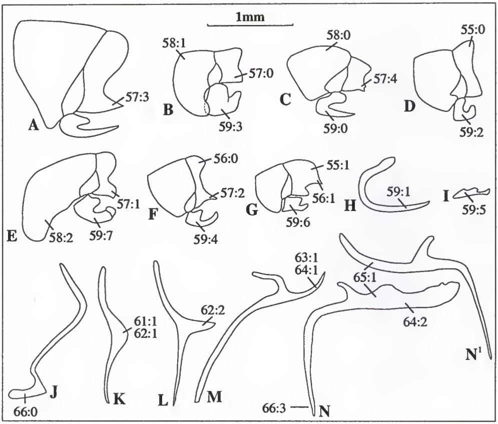

Te
1mm
54:1
Un
Fa
Va
Vi
79:2
Co
Ae
81:1
Pe
44:2
66:1
St
A
51:1
52:1
60:0
81:0
50:D
66:2
B
53:1
C
52:2
60:1
73:2
81:2
50:C
79:7
D

Fig. 292. Representative male genitalic unci (Figs. A-G), falci (Figs. A-I) and vincula (Figs. J-N) for the Theopeiti, illustrating characters 55-65 in Table 9. All structures are figured in lateral view and those in Fig. N in left and right lateral views (marked with a superscript 1). **A**: *Theope matuta heureka*; **B**: *Theope pepo*; **C**: *Theope dabrerae*; **D**: *Theope iani*; **E**: *Theope thootes*; **F**: *Theope discus*; **G**: *Theope wallacei*; **H**: *"Adelotypa" senta*; **I**: *Theope janus*; **J**: *Thisbe irenea* [outgroup taxon]; **K**: *Theope eupolis*; **L**: *Theope publius publius*; **M**: *Theope sobrina*; **N**: *Theope thootes*.



1mm
A
57:3
58:1
57:0
B
59:3
58:0
57:4
C
59:0
55:0
D
59:2
56:0
57:2
F
59:4
57:1
E
58:2
59:7
55:1
56:1
G
59:6
59:1
H
I
59:5
63:1
64:1
65:1
64:2
N¹
62:2
61:1
62:1
J
66:0
K
L
M
66:3
N

Fig. 293. Representative male genitalic valvae for the Theopeiti, illustrating characters 67-70 in Table 9. All structures are figured in lateral view, but those in Figs. T-V are also figured in dorsal view (marked with a superscript 1). **A**: *"Adelotypa" senta*; **B**: *Archaeonympha drepana*; **C**: *"Calociasma" lilina*; **D**: *"Pandemos" godmanii*; **E**: *Theope eurygonina*; **F**: *Theope brevignoni*; **G**: *Theope orphana*; **H**: *Theope hypoleuca*; **I**: *Theope archimedes archimedes*; **J**: *Theope devriesi*; **K**: *Theope eudocia*; **L**: *Theope mundula*; **M**: *Theope sericea*; **N**: *Theope dabrerae*; **O**: *Theope pieridoides*; **P**: *Theope sisemina sisemina*; **Q**: *Theope publius publius*; **R**: *Theope nodosus*; **S**: *Theope thestias*; **T**: *Theope lycaenina*; **U**: *Theope turneri*; **V**: *Theope foliorum*.

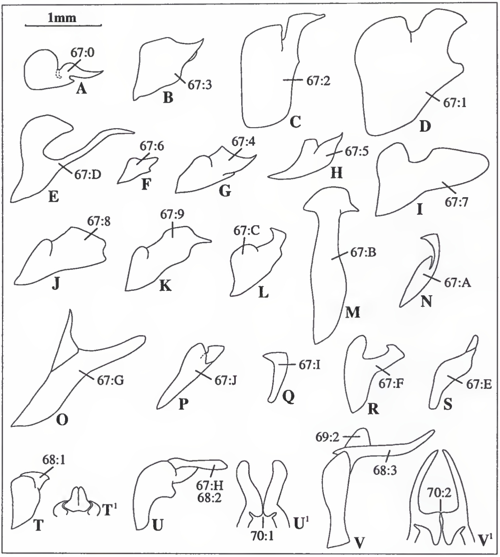

1mm
67:0
A
67:3
B
67:2
C
67:1
D
67:D
E
67:6
F
67:4
G
67:5
H
67:7
I
67:8
J
67:9
K
67:C
L
67:B
M
67:A
N
67:G
O
67:J
P
67:I
Q
67:F
R
67:E
S
68:1
T
T¹
67:H
68:2
U
70:1
U¹
69:2
68:3
V
70:2
V¹

Fig. 294. Representative male genitalic aedeagi and cornuti for the Theopeiti, illustrating characters 71-80, and 82-83 in Table 9. Fig. A (single cornutus) is illustrated in dorsal view, Figs. B-I (aedeagi with cornuti) in lateral view, and Figs. J-K (aedeagi with pedicels) in ventral view. **A**: "*Pandemos*" *godmanii*; **B**: *Thisbe irenea* [outgroup taxon]; **C**: "*Calociasma*" *lilina*; **D**: *Theope orphana*; **E**: *Theope excelsa*; **F**: *Theope mundula*; **G**: *Theope virgilius*; **H**: *Theope leucanthe*; **I**: *Theope foliorum*; **J**: *Theope thootes*; **K**: *Theope zostera*.

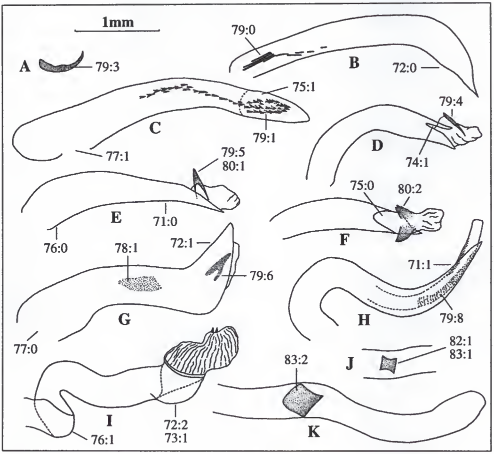

1mm
A
79:3
79:0
B
72:0
75:1
C
79:1
77:1
79:4
D
74:1
79:5
80:1
E
71:0
76:0
75:0
80:2
F
78:1
72:1
79:6
71:1
G
H
79:8
77:0
82:1
83:1
J
83:2
I
72:2
73:1
76:1
K

Fig. 295. Selected female genitalia of the Theopeiti, illustrating characters 87-89, 92-94, and 99-101 in Table 9. Figs. A-D represent all copulatory organs of the genitalia, and Fig. E. represents the posterior end of the corpus bursae in dorsal and lateral views (marked with a superscript 1). **A**: *Theope terambus*; **B**: *Theope devriesi*; **C**: *Theope wallacei*; **D**: *Theope apheles*; **E**: "*Adelotypa*" *senta*. Abbreviations on Fig. A: **Ob** - Ostium bursae; **Db** - Ductus bursae; **Ds** - Ductus seminalis; **Cb** - Corpus bursae; **Si** - Signa.

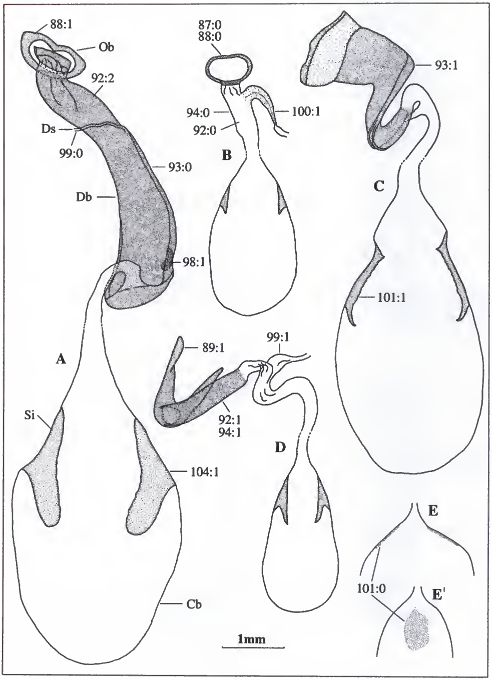

88:1
Ob
92:2
Ds
99:0
93:0
Db
98:1
A
Si
104:1
Cb
87:0
88:0
94:0
92:0
100:1
B
93:1
C
101:1
89:1
99:1
92:1
94:1
D
E
101:0
E'
1mm

Fig. 296. Representative last (eighth) female abdominal tergites (Figs A,B) and posterior female genitalic structures (ostium and ductus bursae - Figs. C-J) for the Theopeiti, illustrating characters 84-87, 90-91, and 95-97 in Table 9. Figs. A,B and J1 are figured in lateral view, Figs. C-E and G-I in dorsal view, and Figs. F and J in ventral view. **A**: *Theope apheles*; **B**: *Theope thootes*; **C**: *Archaeonympha smalli*; **D**: *Archaeonympha drepana*; **E**: *Theope virgilius*; **F**: *Theope tetrastigma*; **G**: *Theope archimedes archimedes*; **H**: *"Adelotypa" senta*; **I**: *Theope kingi*; **J**: *Theope discus*.

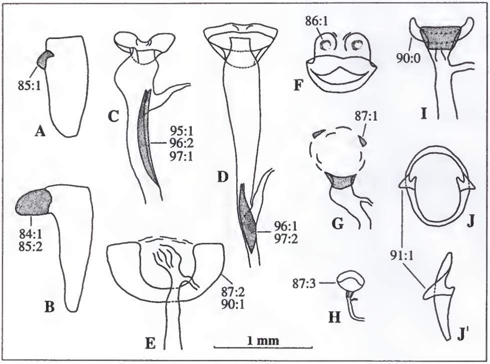
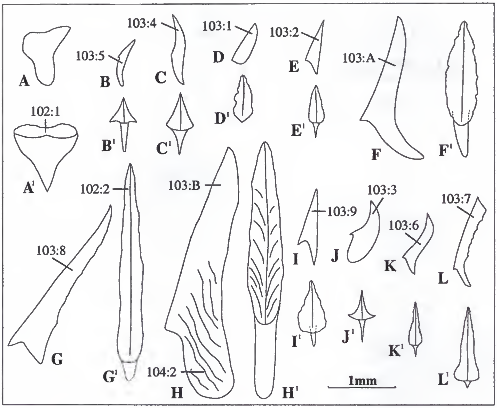

85:1
A
B
84:1
85:2
C
95:1
96:2
97:1
D
96:1
97:2
E
87:2
90:1
1 mm
86:1
F
87:1
G
87:3
H
90:0
I
J
91:1
J'

Fig. 297. Representative female genitalic signae for the Theopeiti, illustrating characters 102-104 in Table 9. All signae are figured in lateral and dorsal view (marked with a superscript 1). **A**: "*Pandemos*" *godmanii*; **B**: *Archaeonympha smalli*; **C**: *Archaeonympha urichi*; **D**: *Theope cratylus*; **E**: *Theope devriesi*; **F**: *Theope kingi*; **G**: *Theope virgilius*; **H**: *Theope basilea*; **I**: *Theope comosa*; **J**: *Theope discus*; **K**: *Theope leucanthe*; **L**: *Theope lycaenina.*



A
A'
102:1
103:5
B
B'
103:4
C
C'
103:1
D
D'
103:2
E
E'
103:A
F
F'
102:2
G'
103:8
G
103:B
104:2
H
H'
103:9
I
I'
103:3
J
J'
103:6
K
K'
103:7
L
L'
1mm

only in the derived half of the genus, from clade 8 onwards, although they are subsequently lost in most species of the "*foliorum* group" (clade 13). Interestingly, in conjunction with several genitalic asymmetries in both sexes, the entire shape of the last tergite in members of the "*theritas* group" (clade 11) is asymmetrical (Fig. 289J). The strongest evidence for the sister group relationship of the two most derived groups in the Theopeiti, the "*thestias*" and "*foliorum* groups" of *Theope* (clades 12 and 13), comes from the presence of a tiny, lightly sclerotised fenestration towards the ventral margin of the last tergite (Fig. 289I), which, as in the invaginations along the ventral margin in certain plesiomorphic groups (character 35) (Figs. 289D,E), is probably spiracular in origin.

The second, and in this instance unique, universal synapomorphy for the genus *Theope* (see Table 10) can be found in the terminal male sternite, which has a sclerotised invagination dorsally that extends to connect to the base of the genital armature (Fig. 291A), to which it is typically attached when the genitalia are dissected out of the abdomen. Dorsal sclerotised invaginations do occur in a few plesiomorphic species of the Theopeiti (e.g. see Fig. 290B) and a few species of the Nymphidiiti, but these are restricted to the posterior half of the sternite and connected to the genital armature only by extensive membraneous tissue. The shape of the last sternite also provides apomorphies for the generic "*lilina* group" and "*Pandemos*" *godmanii* clades (C and D). The main evolutionary trend in terminal sternite structure throughout the large genus *Theope* is the gradual reduction in the ventral element from the typical rectangular shape of most riodinid ventral sclerites in the plesiomorphic half of the genus (clades 1-8) (Fig. 290A), to a tiny vestigial triangle or band in the most derived species groups (clades 10-13) (Figs. 290K,291B,291D); but, paradoxically, there is a concomitant increase in overall structural complexity in the same direction, at least as far as the "*theritas* group" (clade 11), from the simple ribbon-like terminal sternite of the "*nycteis* group" (clade 1)

(Fig. 290C) to the enormous three-dimensional structures of certain "*sericea* group" species (clade 7) (Fig. 290G), and the elongate dorso-lateral projections of the "*sisemina* group" (clade 8) (Fig. 290I). The most bizarre terminal sternite modifications are to be found in the "*theritas* group" of *Theope* (clade 11), in which the dorsal element is asymmetrically produced into a very long left-hand projection and a typically much shorter right-hand projection (see Figs. 290K,L). One species in this group, *Theope sobrina*, possesses perhaps the most formidable array of what are presumably copulatory grappling structures in all the Riodinidae, including a small blunt posterior projection from the last tergite, and elongate, spiky posterior projections from the highly modified last sternite (Fig. 290L), and the valvae and vinculum (Fig. 292M) of the genital armature (see below).

Since the turn of the nineteenth century (e.g. Godman & Salvin, 1879-1901), male genitalia have become the most widely used morphological structures in Lepidopteran classifications at middle and low taxonomic levels. In the Theopeiti, the shapes of the unci, falci, vincula (Fig. 292), aedeagi and internal cornuti (Fig. 294), and particularly the valvae (Fig. 293) provide a wealth of characters that allow the delimitation of species groups and the separation of otherwise superficially similar species. For example, species that have long been confounded with each other, such as *Theope lycaenina* (Fig. 286X) and *Theope wallacei* (Fig. 286Y), actually turn out to have utterly distinctive genitalia that place them in different subgroups of the "*foliorum* group" (clade 13) (Figs. 291D,293T). This is in stark contrast to the sister subtribe Nymphidiiti, whose members exhibit an equally remarkable homogeneity in the male genitalia, especially in the more recently derived terminal clades. The valvae, as their common name suggests, are typically the predominant clasping structures utilised during copulation, and those of, for example, the "*foliorum* group" of *Theope* (clade 13) (Fig. 293U-V) appear to be particularly well adapted to this function. However, as well as having evolved terminal sclerites designed for copulatory clasping, certain members of *Theope*, particularly those in the "*terambus*" and "*theritas* groups" (clades 10 and 11), are extraordinary in possessing variably elongate posterior projections from the upper half of the vinculum (Figs. 292K-N) that have presumably evolved for the same purpose; it is a character rarely seen elsewhere in the family (e.g. in the symmachiine genus *Pirascca* Hall & Willmott (Hall & Willmott, 1996c). One obvious character that distinguishes the subtribes Theopeiti and Nymphidiiti is that all members of the former, except the "*lilina* group", lack an anterior saccus (Fig. 292J) at the ventral base of the vinculum, whereas this structure is present in all but a few plesiomorphic species of the latter. Another is that all species in the Theopeiti possess an incomplete vinculum dorsally, whereas this structure extends around the entire anterior edge of the tegumen in all but a few plesiomorphic genera of the Nymphidiiti. The definitive male genitalic character distinguishing the Theopeiti from the Nymphidiiti is the absence in all its species of dorsal sclerotised tissue (a transtilla) joining the valve tips.

Female genitalia and abdomen

The terminal tergite of the female abdomen exhibits minimal variation compared to that of the male, but a disc at the upper posterior corner does vary in its degree of sclerotisation, and in certain members of the "*theritas* group" (clade 11) of *Theope* its posterior length is also variable (Figs. 296A,B). Female genitalia have historically been utilised in Lepidopteran systematics to a far lesser extent than those of the male. In fact the first classification of the Riodinidae to encompass female genitalic characters was that of Harvey (1987), and very few recent taxonomic publications have included them. This study represents the most extensive review of female genitalia for any single large group of riodinids to date. In the Theopeiti, the female genitalia are more evolutionarily conservative than those of the male and, since they are less structurally complex, exhibit less variation, but the shapes of the ostium bursae (Figs. 295,296) and signae (Fig. 297), and the degree of sclerotisation in the ductus bursae and seminalis (Fig. 295) still provide many species group characters, and, importantly, phylogenetic information at levels above the species group. Indeed, the presence of an elongate, hollow sclerotised structure in the middle of the ductus bursae at the opening to the ductus seminalis (Figs. 296C,D) is a unique universal synapomorphy for the genus *Archaeonympha* (see Table 10) (Hall & Harvey, 1998). No variation could be found in the shape of the papillae anales, and, although some variation occurs in the shape of the corpus bursae, this could not be coded. Anteriorly pointing spines on the inner surface of the corpus bursae, as reported by Robbins (1991) for the eumaeine lycaenid genus *Rekoa* Kaye, were observed in two *Theope* species under a SEM and found to vary in shape and spacing; although these characters would probably provide useful phylogenetic information, it was beyond the scope of this study to examine the corpus bursae of all species under the SEM.

Several broad evolutionary patterns in the group are worthy of mention. The ostium bursae is typically sclerotised only ventrally in the most plesiomorphic groups, but becomes a heavily sclerotised ring in most of the derived groups (Figs. 295,296), and in such groups, notably the "*thestias* group" of *Theope* (clade 12), the shape often becomes more elaborate (Fig. 296J). The degree of sclerotisation in the posterior half of the ductus bursae also increases markedly in the same direction, with heavily sclerotised tubes being prevalent in most members of the "*terambus*", "*theritas*" and "*foliorum* groups" of *Theope* (clades 10, 11 and 13) (Fig. 295). A character state that is not known to occur elsewhere in the Riodinidae is the coiling of this sclerotised tube (posterior half of ductus bursae) in *Theope* species of the "*foliorum* group" (clade 13) (Fig. 295C), which appears to be correlated to a degree with the contorted shape of the male aedeagus. Also of note, is that in most riodinid species the ductus seminalis is a narrow very lightly sclerotised tube, but in the "*pedias*" and "*eudocia* groups" of *Theope* (clades 5 and 6), it is very broad and hardened as it joins to the ductus bursae (Fig. 295B).

Discussion

The riodinid subtribe Theopeiti exhibits perhaps the greatest range of morphological variation for any group of its size in the Riodindae, predominantly between species groups, and thus a wealth of characters have been available for phylogenetic study. Although there is often morphological homogeneity within groups, especially the most derived ones, indicative of recent species radiation, the group is clearly ancient, and based on evidence from Dominican amber, at least 15 or 20 million years old (Iturralde-Vinent & MacPhee, 1996; DeVries & Poinar, 1997). Given the large character set and the high degree of character and bootstrap support for most of the labelled clades, the cladogram in Figure 288 must be regarded as a reasonably robust hypothesis of phylogenetic relationships within the group. However, the support for and resolution of certain tree regions still remains unsatisfactory. The inclusion of the more evolutionarily conservative character set of early stages, if they were ever to become available, might aid in providing better support for deeper nodes (Alexander, 1990; Miller, 1991, 1996), and molecular data might be particularly helpful in resolving sibling species complexes in the most recent lineages (Miller, Brower & DeSalle, 1997). The most prominently unresolved portion of the tree lies in the "*foliorum* group" of *Theope* (clade 13), due largely to the high percentage of unknown females in the group, but since the genitalia of the known females exhibit considerable variation, it is likely that when these unknown females are discovered, their character information will substantially help to resolve the evolution of this derived clade. There are four species in *Theope* that can not be placed in any well defined species group and were placed in Chapter 2 in a miscellaneous section. It should be pointed out that the high number of autapomorphies exhibited by these species means that their exact placement on the tree remains somewhat uncertain, and, in particular, I am not confident that *T. eurygonina* belongs at the very base of *Theope*. Further uncertainty lies in the presented hypothesis of evolutionary relationships between the four plesiomorphic generic clades A-D, due to the paucity of nested synapomorphies for the basal nodes concerned. Only the use of further character sets is likely to resolve these problems.

The topology of the cladogram indicates that several changes in the classification of this group are required. Three generic names are nomenclaturally available for the species included here in the Theopeiti, but as a result of this study, two of those, the genera *Parnes* (clade 1) and *Dinoplotis* (part of clade 2), have been synonymised with the third, *Theope*. The genus *Archaeonympha* has already been described for clade B in Hall & Harvey (1998), but clades A, C and D, containing species currently treated in the polyphyletic genera *Adelotypa*, *Calociasma* and *Pandemos* are still in need of description, work that is currently in progress (Hall, in prep.; Hall & Harvey, in prep.).

CHAPTER 5
CONCLUSIONS

Using one of the largest morphological data sets ever compliled for the Lepidoptera, this study has generated one of the first phylogenies for the butterfly family Riodinidae. A comprehensive cladistic analysis of the subtribe Theopeiti (tribe Nymphidiini) has highlighted the existence of five monophyletic groups worthy of generic status, however, at the outset of this work only the single generic name *Theope* was available. The genus *Archaeonympha* has been described for a few species formerly included in *Theope*, but the remaining three genera are still in need of description (Hall, in prep.). This study has therefore begun the process of creating a natural generic classification for the Riodinidae and bringing the taxonomy of the group into line with modern systematic thinking, a process that is being continued for the sister subtribe Nymphidiiti (Hall, in prep.).

Thirteen monophyletic clades or species groups have been isolated within *Theope* that are largely very well supported by high bootstrap values. The delineation of these has allowed broad conclusions to be made about the biogeography of the group, and contributed to our undertstanding of how constituent species maintain reproductive isolation. The highly resolved phylogeny for this large genus may also prove to be very important for future studies, for example those looking at the evolution of host-plant use and butterfly-ant mutualisms.

The recognition of the genus *Theope* as a monophyletic group containing the species treated in this work has necessitated the synonymy of two genera, *Parnes* and *Dinoplotis*, and the erection of another, *Archaeonympha*. Five species, namely *nycteis*, *brevignoni*, *philotes*, *orphana* and *antanitis*, have been newly brought into combination with *Theope* from three different genera, a total of fifteen species and four subspecies have been described during the course of revisionary work; a number of other taxonomic changes have been made at the species level and below, and for the purpose of nomenclatural stability a total of fifteen lectotypes have been designated.

This study presents the most extensive data set ever compiled for male riodinid perching times and assesses interspecific differences in the perching parameters of time and space, especially in the context of hilltop leks. The evidence strongly suggests that phylogeny has a substantial influence on these parameters, such that species in the same group are more likely to perch at the same height and time than those in other groups. Thus the widely held assumption that differences in the parameters of microhabitat, time and space are alone sufficient to maintain reproductive isolation is shown to be false. The use of pheromones is invoked as an additional, largely overlooked means to maintain reproductive isolation. So little is currently understood about the phenomenon of riodinid lekking that it promises to be a fruitful area of investigation in the future.

APPENDIX A
ERRORS OF IDENTIFICATION OF *THEOPE* IN POPULAR LITERATURE (1886-1997)

Godman and Salvin - Biologia Centrali-Americana. Insecta. Lepidoptera-Rhopalocera (1886: plates 46-47, pp. 481-485)
Plates: **46**. *Theope thootes = Theope phaeo* female; *Theope isia = Theope pedias*; *Theope basilea* male = *Theope bacenis*. **47**. *Theope publius = Theope publius publius*; *Theope hypoxanthe = Theope pedias*; *Theope folia = Theope phaeo*; *Theope herta = Theope foliorum*.
Additional errors in text: *Theope caenina = Theope barea*.

Seitz - The Macrolepidoptera of the World. Vol V. Rhopalocera americana (1920: plates 110A, 138, 143, pp. 699, 705, 722-726)
Plates: **110A**. *Theope colombiana = Theope eurygonina*; *Theope sisemina = Theope sisemina sisemina*. **138**. *Parnes nycteis = Theope nycteis*; *Parnes philotes = Theope philotes*. **143**. *Theope herta = Theope foliorum*; *Theope theritas* is misspelt *Theope thersitas*; *Theope diores = Theope eupolis*;*Theope publius = Theope publius publius*; *Theope talna = Theope eupolis*; *Theope basilea = Theope bacenis*; *Theope matula* [sic] = *Theope matuta heureka*; *Theope folia = Theope phaeo*.
Additional errors in text: **p.705**. *Lemonias antanitis = Theope antanitis*. **p.722**. *Theope eudocia acosma = Theope acosma*. **p. 723**. *Theope eudocia pulchralis = Theope eudocia*; *Theope pedias isia = Theope pedias*; *Theope pedias hypoxanthe = Theope pedias*; *Theope caenina = Theope barea*; *Theope foliorum puntipennis = Theope foliorum*; *Theope foliorum atima = Theope atima*. **p. 724**. *Theope phineus = Theope speciosa*; *Theope virgilius eupolis = Theope eupolis*; *Theope virgilius polimela = Theope virgilius*; *Theope virgilius caerulea = Theope virgilius*; *Theope virgilius nobilis = Theope nobilis*. **p.725**. *Theope apheles sobrina = Theope sobrina*; *Theope thentis* [sic] = *Theope phaeo*; *Theope phaeo folia = Theope phaeo*; *Theope eleutho = Theope bacenis*; *Theope mania = Theope bacenis*; *Theope thebais = Theope archimedes*; *Theope thebais matuta = Theope matuta*; *Theope drepana = Archaeonympha drepana*. **p.726**. *Theope thestias discus = Theope discus*; *Theope thestias decorata = Theope decorata*; *Theope eurygonina colombiana = Theope eurygonina*; *Theope eurygonina sisemina = Theope sisemina sisemina*.

Barcant - Butterflies of Trinidad and Tobago (1970: plates 9, 22, 27, pp. 109-110, 216-219)
Plates: **9**. *Theope syngenes = Theope terambus*; *Theope thootes* male = *Theope phaeo* female; *Theope pedias pedias* male = *Theope pedias* female; *Theope eudocia eudocia = Theope eudocia*. **27**. *Theope barea* female = *Theope aureonitens* male; *Theope apheles = Theope phaeo*; *Theope foliorum*: male is a female.

Lewis - Butterflies of the world (1973: plates 72, 77, 79)
Plates: 72. *Dinoptotis* [sic] *orphana = Theope orphana*. 77. *Parnes nycteis = Theope nycteis*. 79. *Theope matuta = Theope archimedes zyzyxoxyx*; *Theope publius = Theope publius incompositus*; *Theope thestias = Theope decorata*.

de la Maza - Mariposas Mexicanas (1987: plate 50)
Plate: **50**. *Theope diores = Theope eupolis*; *Theope pedias isia = Theope devriesi*.

Vélez and Salazar - Mariposas de Colombia (1991: p. 121)
p. 121. *Theope cratylus* female = *Theope pedias* male; *Theope matuta = Theope archimedes zyzyxoxyx*.

D'Abrera - Butterflies of the Neotropical Region, Part VI. Riodinidae (1994: pp. 992-1003, 1033, 1074)
p. 992. *Theope* ? sp = *Theope pieridoides*. **p. 993**. *Theope eudocia* female = *Theope acosma* male; *Theope punctipennis = Theope foliorum*. **p. 994**. *Theope methemona* female = *Theope wallacei*; *Theope herta = Theope foliorum*; *Theope cacnina* [sic] = *Theope barea*; *Theope* ? sp. = *Theope mundula*; *Theope isia* male = *Theope pedias*; *Theope isia* female = *Theope pseudopedias*. **p. 995**. *Theope hypoxanthe = Theope pedias*; *Theope* ? sp. male = *Theope pepo* female; *Theope* ? sp. female = *Theope comosa*; *Theope* sp. = *Theope pepo*; *Theope* ? sp. nr. = *Theope sericea*. **p. 997**. *Theope theutis = Theope phaeo*; *Theope thootes = Theope sobrina*. **p. 998**. *Theope caerulea = Theope virgilius*; *Theope talna = Theope eupolis*; *Theope folia = Theope phaeo*. **p.999**. *Theope tetrastigma* is misspelt *Theope tetrasigma*; *Theope publius = Theope publius publius*. **p. 1001**. *Theope mania = Theope bacenis*; *Theope drepana = Archaeonympha drepana*; *Theope eleutho = Theope bacenis*. **p. 1003**. *Theope* ? sp. = *Theope christiani*; *Theope columbiana = Theope sisemina tabacona*; *Theope zyzyxoxyx = Theope archimedes zyzyxoxyx*; *Theope thebais = Theope archimedes archimedes*; *Theope thebais* ? Subsp = *Theope matuta heureka*; *Theope urichi = Archaeonympha urichi*; *Theope thestias* male = *Theope decorata* female. **p. 1033**. *Calospila antanitis = Theope antanitis*. **p. 1074**. *Parnes nycteis = Theope nycteis*; *Parnes philotes = Theope philotes*.

DeVries - The Butterflies of Costa Rica and their Natural History. Volume II: Riodinidae (1997: plates 11, 23-25, pp. 239-247)
Plates: **11**. *Parnes nycteis = Theope nycteis*. **23**. *Theope publius = Theope publius publius*; *Theope eleutho = Theope bacenis*. **24**. *Theope matuta = Theope matuta matuta*; *Theope phaeo folia = Theope phaeo*; *Theope pedias*: sexes are transposed; *Theope herta = Theope foliorum*; *Theope decorata*: male is a female.
Additional errors in text: **p.243**. *Theope thebais = Theope matuta matuta*. **p.244**. *Theope matuta = Theope archimedes zyzyxoxyx*; *Theope eudocia pulchralis = Theope eudocia*. **p.245**. *Theope thestias decorata = Theope decorata*. **p.247**. *Theope pedias isia = Theope pedias*.

APPENDIX B
AN ALPHABETICAL LIST OF *THEOPE* DISSECTIONS EXAMINED

Individual entries under each taxon consist of the number of specimens, sex, country of origin followed by state and specific locality if known, collection of origin, a dissection number if applicable, and holotype (HT), lectotype (LT), syntype (ST), and allotype (AT) symbols where applicable. The genitalic preparations of specimens marked with an asterisk are illustrated in Figures 78-260. All dissections were made by the author except the four specimens marked DJH which were done by D. J. Harvey at the AME and USNM.

Taxon	**Dissections examined**
acosma Stichel, 1910	1 male: Ecuador, Napo, Apuya (JHKW); 1 male* & 1 female*: Panama, Chiriquí, Potrerillos (USNM)
amicitiae Hall, Gallard & Brév., 1998	2 males: French Guiana, Cayenne, Galion (MNHN) (FSCA) [HT]*
antanitis (Hewitson, 1874)	1 male*: Bolivia (BMNH) [ST]
apheles Bates, 1868	2 males*: Ecuador, Napo, Chichicorrumi (JHKW); 1 male: Ecuador, Morona-Santiago, Taisha (JHKW); 1 male: Ecuador, Napo, Garzacocha (PJD); 1 male: Brazil, Amazonas, Ega (BMNH) [#4418] [LT]; 1 male & 1 female*: French Guiana, Cayenne, Galion (USNM)
a. archimedes (Fabricius, 1793)	1 male*: French Guiana, Cayenne (USNM); 1 male: Brazil, Amazonas, Tefé (AME) [#7410]; 1 female*: Brazil, Rondônia, nr. Cacaulândia (NSM)
a. zyzyxoxyx D'Abrera, 1994	1 male*: Panama, Canal Zone, Piña (FSCA)
atima Bates, 1868	1 male*: Brazil, Pará, Rio Tapajós (BMNH) [#4099]
aureonitens Bates, 1868	1 male*: Ecuador, Napo, Finca San Carlo (JHKW); 1 male: French Guiana, Cayenne, Rte. de L'est (USNM)
azurea Bates, 1868	1 male*: Ecuador, Napo, Chichicorrumi (JHKW); 1 female*: Peru, San Martín, Pumayacu (AMNH); 1 female: Venezuela, Amazonas, San Carlos (USNM)
bacenis Schaus, 1890	1 male: Mexico, San Luis Potosí, El Salto Falls (FSCA); 1 male*: Mexico, Chiapas, Tuxtla Gutierrez (FSCA); 1 male*: Panama, Canal Zone, Piña (FSCA); 1 female*: Panama, Canal Zone, Piña (FSCA)
barea Godman & Salvin, 1878	2 males: Panama, Canal Zone, Los Ríos (FSCA); 1 male: Panama, Canal Zone, Gamboa (AME); 4 males*: Ecuador, Napo, Finca San Carlo (JHKW); 1 female*: Panama, Panamá, nr. El Llano (USNM)
basilea Bates, 1866	2 males*: Ecuador, Esmeraldas, La Punta (JHKW); 1 female*: Panama, Canal Zone, Piña (FSCA)
batesi Hall, 1998	1 male*: Brazil, Amazonas, Manicoré (MNHN) [HT]; 1 male*: Brazil, Pará, Igarapé-Açu (AMNH); 1 male*: Ecuador, Napo, nr. Misahualli (GWB)
brevignoni (Gallard, 1996)	1 male*: Ecuador, Napo, Finca San Carlo (JHKW)
busbyi Hall, 1998	1 male*: Ecuador, Napo, nr. Misahualli (RCB) [HT]
christiani Hall & Willmott, **repl. n.**	1 male*: Guyana, Upper Takutu/Upper Essequibo, Annai (BMNH) [#3846] [HT]
comosa Stichel, 1911	3 males*: Ecuador, Napo, Río Tiputini (JHKW); 1 female*: Brazil, Rondônia, nr. Cacaulândia (NSM)
cratylus Godman & Salvin, 1886	1 male*: Panama, Canal Zone, Cocoli (AME) [#7411]; 1 male: Colombia, El César, Lake Zapatosa (BMNH) [#4870]; 1 female*: Panama, Canal Zone, Piña (FSCA)
dabrerae Hall & Willmott, 1996	1 male*: Ecuador, Napo, Finca San Carlo (JHKW) [HT]
decorata Godman & Salvin, 1878	1 male: Panama, Chiriquí, Bugaba (USNM); 1 male*: Ecuador, Carchi, nr. Lita (JHKW); 1 female*: Brazil, Rondônia, nr. Cacaulândia (NSM)
devriesi Hall & Willmott, 1996	1 male: Costa Rica, Limón, Guapiles (BMNH) [#3849] [HT]*; 1 male: Panama, Canal Zone (USNM); 1 female*: Panama, Canal Zone, Colón (FSCA) [AT]
discus Bates, 1868	1 male: Ecuador, Napo, Cotundo (AME) [#7413]; 1 male*: Brazil, Pará, Pará (BMNH) [#4417]; 1 female*: Ecuador, Napo, Limoncocha (USNM)
eudocia Westwood, 1851	1 male*: Ecuador, Napo, nr. Misahualli (JHKW); 1 male: Ecuador, Carchi, nr. Lita (JHKW); 1 female: Ecuador, Esmeraldas, La Punta (JHKW); 1 female*: Brazil, Rondônia, nr. Cacaulândia (NSM)
eupolis Schaus, 1890	1 male*: Mexico, Veracruz, Veracruz (FSCA); 1 female*: Mexico, Chiapas, nr. Cintalapa (FSCA)
eurygonina Bates, 1868	1 male: Ecuador, Napo, Finca San Carlo (JHKW); 1 male: Ecuador, Napo, Río Tiputini (JHKW); 1 male: Ecuador, Morona-Santiago, Taisha (JHKW); 1 male* & 1 female*: Ecuador, Napo, Apuya (JHKW)
excelsa Bates, 1868	1 male*: Ecuador, Napo, Río Tiputini (JHKW); 1 female*: Ecuador, Napo, Limoncocha (USNM)

foliorum Bates, 1868	1 male: Panama, Canal Zone (USNM); 1 male: Venezuela, Aragua, Cata Cuyagua (AME) [#7423]; 1 male: Venezuela, Aragua, El Limón (AME) [#7424]; 3 males: Peru, Ucayali, Pucallpa (AME) [#7421, 7422, 7427]; 1 male*: Brazil, Rondônia, nr. Cacaulândia (NSM); 1 male: Brazil, Mato Grosso, Diamantino (USNM); 1 male: Brazil, Espírito Santo, Linhares (AME); 1 male: Trinidad, Tunapuna (AME) [#7425]; 1 male: Trinidad, Trois (AME) [#7426]; 1 female*: Ecuador, Napo, Apuya (JHKW)
galionicus Gallard & Brév., 1989	1 male: Brazil, Amazonas, Ipiranga (MNHN); 1 male* & 1 female*: French Guiana (BMNH) [#4103, 4865]
g. guillaumei Gallard, 1996	1 female*: Brazil, Rondônia, nr. Cacaulândia (NSM)
g. cecropia DeVries & Hall, 1996	1 male*: Costa Rica, Heredia, La Selva (AMNH)
hypoleuca Bates, 1868	1 male: Ecuador, Napo, Apuya (JHKW); 1 male*: Brazil, Pará, Ega (BMNH) [#4096]
iani Willmott & Hall, 1994	3 males: Ecuador, Esmeraldas, La Punta (JHKW) [HT]*; 1 female*: Ecuador, Pichincha, Río Tanti (JHKW) [AT]
janus Bates, 1867	1 male*: Peru, Loreto, Iquitos (MNHN); 1 male: French Guiana, Cayenne, Galion (USNM); 1 female*: Brazil, Maranhão, Mt. Aureos (BMNH) [#4869]
kingi Hall & Willmott, 1996	1 male: Panama, Canal Zone, Piña (AME) [#7418]; 1 male* & 1 female*: Panama, Canal Zone, Gatun (USNM) [HT] [AT]
lampropteryx Bates, 1868	1 male*: Ecuador, Morona-Santiago, Taisha (JHKW)
leucanthe Bates, 1868	1 male: Panama (USNM); 1 male: Venezuela (USNM): 1 male: Ecuador (BMNH) [#4098]; 1 male: Brazil, Pará, Santarem (BMNH) [#4097]; 1 male*: Brazil, Rondônia, nr. Cacaulândia (NSM); 1 male: Brazil, Pernambuco, São Lourenço da Mata (USNM); 1 female*: Panama, Panamá, Bayano (USNM)
lycaenina Bates, 1868	1 male: Panama, Canal Zone, Piña (FSCA); 1 male: Ecuador, Napo, Apuya (JHKW); 1 male* & 1 female*: Brazil, Rondônia, nr. Cacaulândia (NSM)
m. matuta Godman & Salvin, 1897	1 male* & 1 female*: Panama, Canal Zone, Gatun (USNM)
m. heureka Hall **n. ssp.**	1 male*: Ecuador, Esmeraldas, La Punta (JHKW)
methemona Bates, 1868	1 male: Brazil, Pará, Santarem (BMNH) [#4863]; 1 male*: Brazil, Pará, Obidos (MNHN)
mundula Stichel, 1926	4 males*: Ecuador, Napo, Río Tiputini (JHKW); 1 male: Ecuador, Napo, Apuya (JHKW); 1 male: Peru, Huánuco, Río Pachitea (ZMHU) [HT]; 1 male: Honduras, Cortés, La Cambre (BMNH) [#3848]; 1 male: Panama, Canal Zone, Gamboa (AME); 1 male & 1 female: Panama, Panamá, Cerro Campana (USNM); 1 female: Panama, Canal Zone, Piña (FSCA); 1 female*: French Guiana (BMNH) [#4864]
nobilis Bates, 1868	1 male*: Brazil, Pará, Rio Tapajós (BMNH) [#4104] [LT]
nodosus Hall **n. sp.**	2 males: Ecuador, Napo, Finca San Carlo (JHKW) [HT]*
nycteis (Westwood, 1851)	3 males*: Ecuador, Napo, Apuya (JHKW); 1 male: Ecuador, Manabí, Cerro Pata de Pájaro (JHKW); 1 male: Ecuador, Carchi, nr. Lita (JHKW); 1 male: Brazil, Rio de Janeiro, Paneiras (BMNH) [#4875]; 1 female*: Ecuador, Esmeraldas, El Durango (JHKW)
orphana (Stichel, 1911)	1 male*: Brazil, Pará, Massauary (ZMHU) [HT]
pakitza Hall & Harvey, 1998	1 male*: Peru, Madre de Dios, Pakitza (MUSM) [#1996-43 DJH] [HT]
pedias Herrich-Schäffer, [1853]	1 male: Guatemala, Alta Verapaz, Río Polochic Valley (BMNH) [#4100] [ST of *isia*]; 1 male: Guatemala, Izabal, Cayuga (USNM); 1 male*: Ecuador, Morona-Santiago, Bomboiza (JHKW); 1 female*: Brazil, Rondônia, nr. Cacaulândia (NSM)
pepo Willmott & Hall, 1994	2 males* & 1 female*: Ecuador, Carchi, nr. Lita (JHKW)
phaeo Prittwitz, 1865	1 male*: Panama, Canal Zone, Piña (AME) [#7415]; 1 male: Trinidad, St. Annes (AME) [#7416]; 2 males: Ecuador, Napo, Finca San Carlo (JHKW); 2 males & 1 female*: Ecuador, Pichincha, Río Tanti (JHKW)
philotes (Westwood, 1851)	1 male* & 1 female*: Ecuador, Napo, Apuya (JHKW)
pieridoides C. & R. Felder, 1865	1 male*: Ecuador, Bolívar, La Chima (BMNH) [#4860]; 1 male: Trinidad, Hololo (AME) [#4472-DJH]; 1 female*: Trinidad (USNM)
pseudopedias Hall **n.** sp.	1 male* & 1 female*: Guatemala, Izabal, Cayuga (USNM) [HT] [AT]
p. publius C. & R. Felder, 1861	1 male*: Ecuador, Loja, nr. Mácara (JHKW); 1 female*: Panama, Canal Zone, Piña (FSCA)
p. incompositus Hall **n. ssp.**	1 male*: Mexico, Oaxaca, Tapanatepec (AME) [#7417]; 1 male: Mexico, Guerrero, nr. El Treinte (AME) [HT]; 1 female*: Mexico, Guerrero, Acahuizotla (AME) [AT]
sanjuani D'Abrera, 1994	1 male*: Colombia (USNM)
sericea Bates, 1868	1 male: Peru, Madre de Dios, nr. Puerto Maldonado (USNM) [DJH]; 1 male*: Brazil, Amazon (BMNH) [#4101]; 1 male: Guyana, Cuyuni/Mazaruni, Bartica (BMNH) [#4102]
simplicia Bates, 1868	1 male: Brazil, Pará, Pará (BMNH) [#4861]; 1 male*: Brazil, Mato Grosso, Diamantino (USNM); 1 female*: Brazil, Pará, Pará (BMNH) [#4862]
s. sisemina Seitz, 1920	1 male: Ecuador, Sucumbíos, nr. La Bonita (JHKW); 1 male*: Ecuador, Napo, Baeza (JHKW); 1 female*: Ecuador, Napo, Baeza (USNM)
s. tabacona Hall & Willmott, 1996	1 male*: Peru, Cajamarca, Río Tabaconas (BMNH) [#3847] [HT]

sobrina Bates, 1868	1 male: Peru, Loreto, Iquitos (MNHN); 1 male: Peru, San Martín, Juanjui (MNHN); 1 male: Peru, San Martín, Chazuta (MNHN); 1 male*: Brazil, Amazonas, Ipiranga (MNHN); 1 male: Brazil, Rondônia, nr. Cacaulândia (NSM); 1 male & 1 female*: French Guiana, Cayenne, Galion (JHKW); 1 female: French Guiana, Cayenne, Kaw (JHKW); 1 female: Brazil, Pará, Rio Tapajós (BMNH) [#4867] **[ST]**
speciosa Godman & Salvin, 1897	1 male*: Panama (FSCA); 1 female*: Panama, Canal Zone, Piña (FSCA)
sticheli Hall, 1998	1 male*: Brazil, Pará, Itaituba (ZMHU) **[HT]**; 1 male: Ecuador, Napo, Garzacocha (PJD); 1 female*: Brazil, Rondônia, nr. Cacaulândia (NSM) **[AT]**
syngenes Bates, 1868	1 male* & 1 female*: French Guiana, Cayenne (USNM)
terambus (Godart, [1824])	1 male: Brazil, Espírito Santo, Conceicão de Barra (AME) [#7420]; 1 male*: Brazil (USNM); 1 male: French Guiana, Cayenne (USNM); 1 male: Trinidad, Port of Spain (AME) [#7414]; 1 female: Brazil, Rondônia, nr. Cacaulândia (NSM)
tetrastigma Bates, 1868	1 male*: Ecuador, Napo, Río Tiputini (JHKW); 1 female*: Ecuador, Napo, Finca San Carlo (JHKW)
theritas Hewitson, 1860	1 male: Brazil, Amazonas, Tefé (AME) [7419]; 1 male: Brazil, Amazonas, Manicoré (ZMHU); 1 male: Brazil, Amazon (MNHN); 1 male*: Brazil, Rondônia, nr. Cacaulândia (NSM); 1 male: No locality data (MNHN); 1 female*: Brazil, Pará, Pará (BMNH) [#4866]
thestias Hewitson, 1860	1 male*: Brazil, Rondônia, nr. Cacaulândia (NSM); 1 male: Brazil, Santa Catarina, Joinvile (AME) [#7412]; 1 female*: Brazil, Paraná, nr. Ponta Grossa (USNM)
thootes Hewitson, 1860	2 males: Peru, Loreto, Iquitos (MNHN); 1 male: Brazil, Amazonas, Ipiranga (MNHN); 1 male: Brazil, Pará, Rio Tapajós (BMNH) [#4419]; 1 male: French Guiana, Cayenne, Galion (USNM); 3 males* & 1 female*: Brazil, Rondônia, nr. Cacaulândia (NSM); 1 female: Brazil, Pará, Pará (BMNH) [#4868] **[ST]**
turneri Hall & Austin, 1997	1 male*: Brazil, Rondônia, nr. Cacaulândia (NSM) **[HT]**
villai Beutelspacher, 1981	1 female*: Mexico, Guerrero, Acahuizotla (AME)
virgilius (Fabricius, 1793)	1 male: Mexico, San Luis Potosí, El Salto Falls (FSCA); 1 male: Costa Rica, Puntarenas, Palmar Norte (FSCA); 1 male: Panama (FSCA); 1 male: Ecuador, Loja, nr. Mácara (JHKW); 1 male: Ecuador, Pichincha, Tinalandia (FSCA); 1 male*: Ecuador, Napo, Río Tiputini (JHKW); 1 male: Ecuador, Napo, Finca San Carlo (JHKW); 1 female*: Ecuador, Napo, Tena (JHKW); 1 female: Mexico, Chiapas, Tuxtla Gutierrez (FSCA)
wallacei Hall, 1998	2 males: Peru, Madre de Dios, Pakitza (USNM) [1998-6&7 DJH]; 1 male: French Guiana, Cayenne, Cayenne (USNM); 2 males & 1 female*: Panama, Canal Zone, Piña (FSCA) **[HT]*** **[AT]**
zostera Bates, 1868	1 male*: Ecuador, Napo, Apuya (JHKW)

Appendix C. Character matrix for the 75 species in the subtribe Theopeiti and the outgroup taxon *Thisbe irenea*. Missing data are represented by a "?".

	5 10 15 20 25 30 35 40 45 50
Thisbe irenea	00000000000000000000000000000000000000000000000000000
"Adelotypa" senta	00001000000000000000010000000000010000000000000000110
Archaeonympha drepana	?0100000000000000000010000000000021000001000000000110
Archaeonympha urichi	?010?0??000???00000001000000000?02???????????????????
Archaeonympha smalli	?0000000000000000000010000000000021000001000000000110
"Calociasma" lilina	00000100000000000000000000000000020000001011010001000
"Calociasma" sp. n.	?00001000000000000000000000000000?????????11010001???
"Pandemos" godmani	10000000000000000000000000000000021000000011000001110
Theope eurygonina	10000000000000000001000000000000020000000012000124110
Theope nycteis	10003000000000000011000001011000020000000012000002110
Theope brevignoni	10003000000000000011000001011000020000000012000002110
Theope philotes	10003000000000000001000001011000020000000012000002110
Theope tetrastigma	10003000000000000001000001000000022000000012000113110
Theope orphana	?0003000000000000001000001010000022000000012000113110
Theope simplicia	?0000000000000000001000000001???00020000000012000113110
Theope hypoleuca	10000000000000000001000000001???00022000000012000113110
Theope azurea	10000000000110000001000000001???00020000000012000113110
Theope archimedes	10000000000000000101000000000000120000000012000113110
Theope matuta	10000000000000000101000000000000120000000012000113110
Theope pedias	10000000001110000001000000001???01020000000012000124110
Theope pseudopedias	?0000000000110000001000000001???01020000000012000124110
Theope devriesi	10000000001131000001000000001???00020000000012000124110
Theope pepo	10000000001131000001000000001???00020001000112000124110
Theope eudocia	10002000000110000001000000001???01020000000012000125110
Theope acosma	10002000000110000001000000001???01020000000012000125110
Theope barea	10000010000110000001000000001???00020000000012000125110
Theope mundula	10000010000110000001000000001???00020000000012000125110
Theope excelsa	10000000000110000001000000001???00020000000012000124110
Theope kingi	?0000000000110000001000000001???00020000000012000124110
Theope aureonitens	10000010000120000001000000001???00020000001012000126110
Theope galionicus	10000000000120000001000000001???00020000001012000126110
Theope dabrerae	10000000000120000001000000001???00020001000012000124110
Theope sericea	10000000000120000001000000001???00020001000012000124110
Theope lampropteryx	10000000000120000001000000001???00020001000012000124110
Theope speciosa	10000000001000000001000000000000020001000112000124111
Theope pieridoides	10000000000000000001000000001???00020000001012000129111
Theope cratylus	10000000000000000001000000000000020000011101200012 8111
Theope sisemina	10000000000000000001001000000000020000011301200012 8110
Theope antanitis	?0000000000000000001001000000000020000011311200012 8110
Theope iani	11000000000000000001000000000110020000011101200000 7111
Theope villai	?0000000100000000001000000000?100?0000??201200000 7???
Theope virgilius	10000000100000000001000000000110020000011101200000 7111
Theope eupolis	10000000000000000001000000000110020000011101200000 7111
Theope nobilis	10000010000110000001000000000110020000011301210000C111
Theope publius	10000010100000000001000110000110020000011301210000C111
Theope sanjuani	?0000010?00000000001000110000110020000011301210000C111
Theope terambus	10000010100000000001000120000110020000011301210000C111
Theope syngenes	10000010100000000001000120000110020000011301210000C111
Theope bacenis	10000010100000000001100120000110020000011301210000C111
Theope basilea	10000010100000000001100120000110020000011301210000C111
Theope comosa	11000001010000000001000000000010020010113112101 00A110
Theope zostera	11000000010000000001000000001???00020000123112101 00A110
Theope nodosus	110000000?0000000001000000001???00020010113112101 00A110
Theope phaeo	11010001010000000001000000000000020010123112101 00A110
Theope theritas	11000001010000000001000000000000020010123112101 00A110
Theope thootes	11000001010000000001000000000000020010123112101 00A110
Theope apheles	11000001010000000001000000001???02020010123112101 00A110
Theope sobrina	11000001010000000001000000000002020000113112101 00B110
Theope janus	10000000000000011001000000001???00020100113112100 00D110
Theope guillaumei	10003000000000011001000000001???00020100113012100 00D110
Theope discus	10010000000000111001000000001???00020100113012100 00D110
Theope thestias	10010000000000112001000000001???00020100113012100 00D110
Theope decorata	10010000000000112001000000001???00020100113012100 00D110
Theope lycaenina	10000000000000000001000000000000020100000012100 00C110
Theope leucanthe	10000000000000000001000000000000020100000112100 00C110
Theope amicitiae	10000000000000000001000000000000020100001112100 00C110
Theope gallardi	?0000000000000000001000000000000020100000112100 00C110
Theope methemona	?0000010000000000001000000000000020100000112100 00C110
Theope sticheli	10000000000000000001000000000000020100000112100 00C110
Theope busbyi	10000000000000000001000000000000020100000112100 00C110
Theope turneri	?0000000000000000001000000000000020100000112100 00C110
Theope batesi	10000000000000000001000000001???00020100111112100 00C110
Theope atima	?0000000000000000001000000000000020100113112100 00C120
Theope foliorum	10000000000000000001000000000000020100111112100 00C120
Theope wallacei	10000000000000000001000000000000020100001112100 00C120
Theope pakitza	?0000000000000000001000000001???00020100001112100 00C120

	55 60 65 ?0 ?5 80 85 90 95 100
Thisbe irenea	00000000000000000000000000000000000000000000000000
"Adelotypa" senta	0000010000003000000000008000000003???00000000000000
Archaeonympha drepana	10000000000033000000000080000111000000001120001240
Archaeonympha urichi	?????????????????????????????1110000000011200012 40
Archaeonympha smalli	10000000000033000000000080000111000000001210001250
"Calociasma" lilina	00000000000002000000101010100000000000001000001100
"Calociasma" sp. n.	?00000000000020000001010101000??????????????????????
"Pandemos" godmani	00000000000031000000000030100000000000000000001100
Theope eurygonina	1000000000003D000000000080000000002??000000000002000
Theope nycteis	00000000000036000000000080000000002??000000000001210
Theope brevignoni	1000000000003600000000008000?????????????????????
Theope philotes	00000000000036000000000080000000002??000000000001210
Theope tetrastigma	10000000000034000000100040000001000000000000001210
Theope orphana	1000000000003400000010004000?????????????????????
Theope simplicia	10000000000036000000000080000000002??000000000001210
Theope hypoleuca	1000000000003500000000008000?????????????????????
Theope azurea	10000000000036000000000080000000002??000000000001210
Theope archimedes	1003000000003?000000000080000000001??000000000001220
Theope matuta	1003000000003?000000000080000000001??000000000001220
Theope pedias	10000000000038000000000080000110000000000000011220
Theope pseudopedias	10000000000038000000000080000110000000000000011220
Theope devriesi	10001300000038000000000080000110000000000000011220
Theope pepo	10001300000038001000000080000110000000000000011220
Theope eudocia	10040000000039000000100080000110000000000000011210
Theope acosma	10040000000039000000100080000110000000000000011210
Theope barea	1004000000003C00000000005210011 02??0000000000012A0
Theope mundula	1004000000003C0000000000521001102??0000000000012A0
Theope excelsa	1004000000003C0000000000511001102??0000000000012A0
Theope kingi	1004000000003C0000000000511001102??0000000000012A0
Theope aureonitens	1004000000001A000000000080100?????????????????????
Theope galionicus	1004000000001A0000000000801001102??0000000000012A0
Theope dabrerae	1004000000001A000000000080100?????????????????????
Theope sericea	1004000000001B000000000020100?????????????????????
Theope lampropteryx	1004000000001C000000000080100?????????????????????
Theope speciosa	10000000000038000000000080000110000000000000011210
Theope pieridoides	1000000000003G000000000080000110000001000000001210
Theope cratylus	1000000000003F000000000080000110000001000000001210
Theope sisemina	1004000000003J001000000080000 1100??00100000000 1210
Theope antanitis	1004000000003J00100000008000?????????????????????
Theope iani	10000201100031000100000180000 1102??00000000000 1210
Theope villai	1000000110003I0001000001800000002??000000000001280
Theope virgilius	10000001100031000100000180000000 02??10000000000 1280
Theope eupolis	10000001100031000100000180000000 02??10000000000 1280
Theope nobilis	1000000120003100010000016000?????????????????????
Theope publius	100000012000310001000001600000000100000000000012B1
Theope sanjuani	1000000120003100010000016000?????????????????????
Theope terambus	100000012000310001000001600000000100010000010012B1
Theope syngenes	100000012000310001000001600000000100010000010012B1
Theope bacenis	100000012000310001000001600000000100000000000012B2
Theope basilea	100000012000310001000001600000000100010000000012B2
Theope comosa	10010?0000003F00100000008001211000000000000000 1290
Theope zostera	100107000110 3F00100001008001 1?????????????????????
Theope nodosus	1001070001103F001000010080011?????????????????????
Theope phaeo	10012?0001113F00100001008001211000000000000000 1290
Theope theritas	1001270001213F00100001008001212000000101000010 1290
Theope thootes	10012?0001213F00100001008001212000100101000010 1290
Theope apheles	10012?0001213F00100001008001211000100101000010 1290
Theope sobrina	1001070001103F00100001008001211000100101000010 1290
Theope janus	1002050000002E00100001008000011000001000000000 1210
Theope guillaumei	1002040000002E00100000008000011000001000000000 1210
Theope discus	1002040000002E00100000008000011000001000000000 1230
Theope thestias	1002040000002E00100000008000011000001000000000 1230
Theope decorata	1002040000002E00100000008000011000001000000000 1230
Theope lycaenina	1000001000003H11100001008000011000000110000000 1270
Theope leucanthe	1000061000003H21100001008000011000000110000000 1260
Theope amicitiae	1100061000003H2110000100 80000?????????????????????
Theope gallardi	1100061000003H211000010080000?????????????????????
Theope methemona	1100061000003H211000010080000?????????????????????
Theope sticheli	1100061000003H21100001008000011 02??00100000000 1260
Theope busbyi	1100061000003H211000010080000?????????????????????
Theope turneri	1110061000003H211000010080000?????????????????????
Theope batesi	1110061000003H2110000100?0000?????????????????????
Theope atima	1110061000003H2210000100?0000?????????????????????
Theope foliorum	1110061000003H3212100100?020011000000110000000 12?0
Theope wallacei	1110061000003H2212200100?020011000000110000000 1270
Theope pakitza	1110061000003H2212200100?0200?????????????????????

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BIOGRAPHICAL SKETCH

Jason Piers Wilton Hall was born on January 23rd 1972 in Bristol, England. From an early age, his father instilled in him a great sense of wonder and enthusiasm for the natural world, especially butterflies, and as a young boy he was fortunate enough to travel several times to the tropics. These were experiences that would change his life. He graduated from the private school Clifton College, Bristol, in 1990 and went up to St. John's College, Oxford, the same year to begin a bachelor's degree in Zoology. From the age of 17 onwards he has spent an average of 3 months each year studying butterflies in the field, in Africa, South America and the Orient, but co-leading a joint Oxford-Cambridge expedition to Ecuador in 1993, after graduating from Oxford with BA and MA honours degrees in that year, irrevocably focused his research attention on the South American continent.

In order to continue research on Neotropical butterflies and pursue the goal of writing a comprehensive field and natural history guide to the butterflies of Ecuador, he came to Gainesville, USA, in January 1994, to complete a Ph.D degree in Entomology under Dr. T. C. Emmel. During his time as a graduate student, he has continued to conduct field research in Ecuador and museum research throughout Europe and North America, utilising a number of grants, most notably a three year National Geographic Society Research and Exploration Grant awarded jointly to himself and his long-standing friend and co-worker Keith R. Willmott. As a result of this work, he has published nearly 20 scientific papers on butterfly systematics and ecology, many with Keith R. Willmott, and upon graduation he hopes to continue forging a career as an evolutionary biologist, focusing on the butterfly family Riodinidae.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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Thomas C. Emmel, Chair
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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Lee D Miller

Lee D. Miller
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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